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Gross Morphological Studies of the Reproductive System in Representative North American Crane Flies (Diptera: Tipulidae) ¹

BY

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INTRODUCTION

The purpose of this study was to investigate the gross anatomical features, both internal and external, of the terminal abdominal segments in a representative sample of the North American tipuline fauna.

A search of the literature concerning the anatomy of the reproductive system in the dipterous family Tipulidae has shown that aside from the recent work of Byers (1961) on the genus *Dolichopeza*, *Tipula oleracea* is the only member of the Tipulinae in which the entire male and female reproductive system had been treated. In 1924 Bodenheimer summarized existing knowledge of the anatomy of *Tipula oleracea*.

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MATERIALS AND METHODS

Table I gives the names of the species of Tipulinae used in this study. Where only dried specimens were available, they were cleared in dilute (10%) potassium hydroxide, then dissected and observed in glycerine with a compound binocular microscope; specimens preserved in alcohol or Kahle's solution were not treated with potassium hydroxide. The flies were usually studied using a magnification of 100 diameters. In a few instances a phase contrast microscope giving magnifications up to $1164\times$ was used.

Live specimens were preserved either in 80% to 95% ethyl alcohol or in Kahle's solution; however, no final decision as to the greater worth of either as a preservative for gross morphological studies can be made at present. Specimens dissected alive in water and then transferred to alcohol (80-95%) after being opened were by far the best for gross observations. A technique which facilitates to some degree dissection of the semen pump was developed. The semen pump and its immovable apodemes and the intromittent organ were dissected out and transferred to a weak solution of chloral hydrate (one or two drops of chloral hydrate to approximately twice as much water) for one or two minutes and then removed. This procedure softens the sclerotized sheath surrounding the semen pump, from which the immovable apodemes develop, so that they can more easily be removed. In addition the sclerotized wall of the pump itself becomes less brittle and more easily handled for dissection, which proves in any case a very difficult task. Caution in timing must be observed, for too much time in chloral hydrate makes the sclerotized pump pulpy and virtually impossible to dissect.

Drawings were prepared in three ways: 1) squared grid paper 2) camera lucida and 3) microprojector. The squared grid paper method proved best for the external anatomy, while the microprojector was best for internal anatomy.

All the included figures are at least somewhat schematic, and some, as noted in the captions, are entirely so. In all the figures the letters T and S are used as abbreviations for tergum and sternum respectively. It was found important to record the type of preservation or condition of specimens from which drawings were made, for a fly that has dried frequently becomes distorted. An attempt to see all the features available in such a specimen without first relaxing it in some way and perhaps without dissection

fails more often than it succeeds. Taxonomists have often been loathe to dissect specimens, yet as Snodgrass (1904) pointed out very appropriately, "If drawings and descriptions are made of the removed parts, then the mutilated specimen has certainly done more for science than the perfect one can ever do."

TABLE I

Species studied:

An asterisk after the sex indicates the use of material preserved in liquid.

Dolichopeza (oropeza) carolus Alexander, male *, female *
Dolichopeza (oropeza) tridenticulata (Alexander), male *, female *
Brachypremna dispellens (Walker), male, female
Megistocera longipennis (Macquart), male
Ctenophora apicata (Osten Sacken), male
Ctenophora vittata Meigen (= *angustipennis* Loew), male
Tanyptera topazina (Osten Sacken), male, female

NOTE: The specimen studied was identified as *topazina*. There is need for a reworking of the three species in the genus *Tanyptera* which occur in the United States. All may be synonymous, and if this is the case, *fumipennis* (Osten Sacken) is the valid name.

Prionocera oregonica Alexander, male *, female *
Longurio (Longurio) testaceus Loew, male
Holorusia (Holorusia) grandis Bergroth, male *, female *
Nephrotoma altissima erythrophrys (Williston), male
Nephrotoma breviorcornis (Doane), male
Nephrotoma euceroideus Alexander, male *, female *
Nephrotoma ferruginea (Fabricius), male *, female *
Nephrotoma lugeus (Loew), male
Nephrotoma macrocera (Say), male, female *
Nephrotoma polymera (Loew), male
Nephrotoma punctum (Loew), male
Nephrotoma xanthostigma (Loew), male
Tipula (Trichotipula) oropezoides Johnson, male *
Tipula (Trichotipula) macrophallus (Dietz), male, female
Tipula (Nobilotipula) nobilis Loew, male, female
Tipula (Nippotipula) abdominalis (Say), male, female
Tipula (Vestiplex) fultonensis Alexander, male *, female
Tipula (Arctotipula) dickinsoni Alexander, male
Tipula (Arctotipula) plutonis absaroka Alexander, male
Tipula (Yamatotipula) albocaudata Doane, male *, female *
Tipula (Yamatotipula) caloptera Loew, male, female
Tipula (Yamatotipula) concava Alexander, male
Tipula (Yamatotipula) dejecta Walker, male, female
Tipula (Yamatotipula) furca Walker, male *, female *
Tipula (Yamatotipula) jacobus Alexander, male, female
Tipula (Yamatotipula) ludoviciana Alexander, male
Tipula (Yamatotipula) sayi Alexander, male, female
Tipula (Yamatotipula) spernax Osten Sacken, male, female
Tipula (Yamatotipula) subcluta Johnson, male

TABLE 1—*Concluded*

<i>Tipula</i> (<i>Yamatotipula</i>) <i>sulphurea</i> Doane, male, female
<i>Tipula</i> (<i>Yamatotipula</i>) <i>tephrocephala</i> Loew, male, female
<i>Tipula</i> (<i>Yamatotipula</i>) <i>tricolor</i> Fabricius, male, female
<i>Tipula</i> (<i>Tipula</i>) <i>cunctans</i> Say, male
<i>Tipula</i> (<i>Tipula</i>) <i>spenceriana</i> Alexander, male
<i>Tipula</i> (<i>Tipula</i>) <i>pendulifera</i> Alexander, male
<i>Tipula</i> (<i>Schummelia</i>) <i>hermannia</i> Alexander, male, female
<i>Tipula</i> (<i>Oreomyza</i>) <i>alia</i> Doane, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>angulata</i> Loew, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>appendiculata</i> Loew, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>borealis</i> Walker, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>doanei</i> Dietz, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>coloradensis</i> Doane, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>fallax</i> Loew, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>inyoensis</i> Alexander, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>latipennis</i> Loew, male *, female *
<i>Tipula</i> (<i>Oreomyza</i>) <i>pseudotruncorum</i> Alexander, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>shoshone</i> Alexander, male
<i>Tipula</i> (<i>Oreomyza</i>) <i>trivittata</i> Say, male, female
<i>Tipula</i> (<i>Hesperotipula</i>) <i>trypetophora</i> Dietz, male *, female *
<i>Tipula</i> (<i>Eumicrotipula</i>) <i>chiricahuensis</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>albofascia</i> Doane, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>armata</i> Doane, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>australis</i> Doane, male, female
<i>Tipula</i> (<i>Lunatipula</i>) <i>barbata</i> Doane, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>bicornis</i> Forbes, male *, female *
<i>Tipula</i> (<i>Lunatipula</i>) <i>dietziana</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>disjuncta</i> Walker, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>dorsimacula</i> Walker, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>duplex</i> Walker, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>flavibasis</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>fuliginosa</i> (Say), male
<i>Tipula</i> (<i>Lunatipula</i>) <i>incisa</i> Doane, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>macrolabis</i> Loew, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>mohavensis</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>morrisoni</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>pleuracacula</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>rabiosa</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>rangiferina</i> Alexander, male
<i>Tipula</i> (<i>Lunatipula</i>) <i>triplex</i> Walker, male *, female *
<i>Tipula</i> (<i>Lunatipula</i>) <i>unicincta</i> Doane, male, female *

TERMINOLOGY

Published observations concerning the reproductive system of crane flies date back to the works of Reaumur (1740), Dufour (1851) and Westhoff (1882). While the bibliography does not claim to be exhaustive, it contains references to the major works concerning this topic. Since the various authors have often acted

independently in their use of terms for the genitalic parts, much terminological confusion exists. Tables II and III explain the equivalents in usages of authors. These tables include terms for those parts of the reproductive apparatus that are visible without dissection or treatment with a clearing solution; three exceptions are the semen pump, its associated apodemes and portions of the vaginal apodeme. The reader should note that while the descriptions of such workers as Alexander and Byers are sound from the descriptive standpoint, the terminology used by these workers is basically taxonomic and does not pretend to be that of the morphologist.

TABLE II.—Terminological Equivalents for Male Abdominal Structures

(For notes see end of table.)

Frommer	Westhoff (1882) ¹	Snodgrass (1904)	Wesche (1906) ³	Berlese (1909)	Bodenheimer (1924)	Sellke (1936)
1) 1st abdominal segment	1st abdominal segment	1st abdominal segment	Had the segments in Wesche's figures been labeled, his terminology would probably be comparable to mine.	2nd abdominal segment (1st lost)	2nd abdominal segment (1st lost according to Berlese)	2nd abdominal segment (1st lost according to Berlese)
2) 8th tergum	Lamella basalis sup ^{ra}	8th tergum		9th tergum	9th tergum	9th tergum
3) 8th sternum	Lamella basalis infer ^a	8th sternum		9th sternum	9th sternum	9th sternum
4) 9th tergum	Lamella terminalis sup ^{ra}	9th tergum		10th tergum	10th tergum (not labelled in his figure)	10th tergum
Tip of 9th tergum which may take on various shapes	Processus der lamella terminalis sup ^{ra}			Cerci	Dreieckige Platten	Lamella terminalis sup ^{ra}
5) 9th sternum	Lamella terminalis infer ^a	9th sternum		10th sternum (= perianthridio; labelled p ₁ should have been pr)	10th sternum	10th sternum
Fragmenta (= discrete sclerotized areas of the 9th sternum)						
6) Anal tubercle (= ? 10th and 11th segments)		Anal tube, but restricted to segment 10	Anal tube, but restricted to segment 10	11th segment	Analkegel (Since Bodenheimer follows Berlese's interpretation he may have thought the Analkegel represented the 11th segment)	
Dorsal or dorsolateral plates of the anal tubercle				11th tergum		
7) Sclerotizations in the walls of the genital sac, such as the "epimere" (Rees & Ferris, 1939)	Adminiculum und vesicula verbindener Bugel	V-shaped bar in roof of genital chamber lying between posterior arms (labelled a) of central vesicle		11th sternum (= epimere Rees & Ferris, 1939)	Recognizes structure but does not agree with Berlese's interpretation	

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*
(For notes see end of table.)

Frommer	Westhoff (1882) ¹	Snodgrass (1904)	Wesche (1906) ²	Berlese (1909)	Bodenheimer (1924)	Sellke (1936)
8) Basimere(s)	Appendices superae	"Pleura" ²	Forceps	Appendici	Forceps superiores	Appendix supeta
9) Telomere(s)	NOTE: Westhoff did not use a single term to embrace the appendices intermediae and the pars.	Apical appendages NOTE: Three divisions of the inner apical (inner telomere) appendage were recognized.	Forceps superior	Appendici 1 (labelled a)	Forceps inferiores	Appendix intermedia (= Begattungsklammer): composed of pars prima, secunda, tertia and quarta
Outer telomere	Appendices intermediae		Forceps inferior	Recognized divisions called appendici (labelled a2-a4)		
Inner telomere	Pars (1, 2, 3, and 4 = division of inner telomere)	Guard of the penis (= penis sheath = 1st gonapophyses, includes lateral arms)	Penis sheath	Appendici 5 (labelled a5)	Penisscheide (adminiculum, theca)	Adminiculum
10) Adminiculum	Adminiculum					
Lateral arms of adminiculum	Arme des Adminiculis		Double apodemes			Arm (= Chitinplatte)
11) Anterior continuations of the lateral adminicular arms		2nd gonapophyses				
12) Semen pump (vesica)	Vesicula centralis	Central vesicle	Sacculus ejaculatorius	Perifallo (figured this upside down)	Sacculus ejaculatorius	
Compressor apodeme	Spatha	Apodeme	Ejaculatory apodeme	Part of perifallo	Spatha, ejaculatory apodeme	Penis
13) Aedeagus	Ruthenscheide (= integumentum, vagina)	Penis	Penis (= flagellum)	Verga flagelliforme		

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*
(For notes see end of table.)

Frommer	Westhoff (1882) ¹	Snodgrass (1904)	Wesche (1906) ²	Berlese (1909)	Bodenheimer (1924)	Selke (1936)
14) Extended endophallus	Glans (= austulpharen Eichel)					
15) Immovable apodemes	Auriculae vesiculacentralis	Arms (labelled a)	Processes fused to sacculus ejaculatorius	Part of perifallo NOTE: Berlese's figure shows no separation of apodemes and semen pump	Auriculae vesiculacentralis Styli	
Anterior apodemes						
Posterior apodemes	Styli	Arms (labelled b)			Membrane hyalina	
16) Genital sac (= walls of genital chamber)	Membrana hyalina	Genital chamber				Opening of genital sac (= Genitalhöhle)

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*
(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	(Snodgrass (1957)	Byers (1961) *
1) 1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment
2) 8th tergum	8th tergum	8th tergum	8th tergum	8th tergum	8th tergum
3) 8th sternum	8th sternum	8th sternum	8th sternum	8th sternum	8th sternum
4) 9th tergum	9th tergum	9th tergum	9th tergum	9th tergum	9th tergum
Tip of 9th tergum which may take on various shapes	Median lobes of 9th tergum		Process		
5) 9th sternum	9th sternum	9th sternum	9th sternum	9th sternum	9th sternum
Fragmenta (= discrete sclerotized areas of the 9th sternum)	Fragmenta				
6) Anal tubercle (= ? 10th and 11th segments)	Proctiger (= 10th and 11th segments)	Proctiger or "anal segment" (= united 10th segment with cercus-bearing 11th segment)	Anal tube	Snodgrass (1935) 10th segment alone	Anal segment, 10th segment. NOTE: Evidence for an eleventh tergum is mentioned.
Dorsal or dorsolateral plates of the anal tubercle	10th tergum				
7) Sclerotizations in the walls of the genital sac, such as the "epimere," (Rees & Ferris, 1939)	Epimere				Not found in <i>Dolichopeza</i> as it is in <i>Tipula triplex</i> but may be of the same origin as the ad-minicular rods

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*
(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	(Snodgrass (1957)	Byers (1961) ^a
8) Basimere(s)	Coxopodite	Basimere	Basistyle ^b	Basimere (phallic lobe origin, from parameres)	Basistyle
9) Telomere(s)	Style	Distimeres or dististyles	Dististyle	Telomere (phallic lobe origin, from parameres)	Outer dististyle
Outer telomere		Outer distimere	Outer dististyle	Outer telomere	
Inner telomere		Inner distimere	Inner dististyle	Inner telomere	
10) Adminiculum	Hypomere	See note 4	Sometimes referred to as aedeagus; when highly developed and incorporated with the gonapophyses = phallosome	Adminiculum	Adminiculum
Lateral arms of adminiculum	Included in hypomere				
11) Anterior continuations of the lateral adminicular arms					
12) Semen pump (vesica)	Basal bulb of penis				Adminicular rods
Compressor apodeme					Vesica
13) Aedeagus	Penis	Aedeagus: formed by the union of paired penis or aedeagal valves (= mesomeres)	Aedeagus	Aedeagus (phallic lobe origin, from fused mesomeres)	Compressor apodeme
					Penis

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Concluded*

(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	Snodgrass (1957)	Byers (1961) ^a
14) Extended endophallus					
15) Immoveable apodemes	Figured but not given specific names				Anterior apodemes
Anterior apodemes					Posterior apodemes
Posterior apodemes					
16) Genital sac (= walls of genital chamber)	Genital sac				Genital sac, membranous sac

1. Westhoff (1882) used the term hypopygium for segments eight and nine and overlooked the basimeres. He named intersegmental appendages between the eighth and ninth sterna according to whether they are simple or divided as appendix basalis simplex or appendix basalis duplex. The term indistum probably refers to membrane-like evaginations at the base of the adminiculum.
2. Snodgrass (1904) used the term pleura with caution and made it clear that the term was chosen only because of the location of the structures.
3. Wesche's (1906) figure of *Tipula olivacea* is upside down.
4. Crampton (1942) discussed the term adminiculum as used by Westhoff (1882). As he interpreted Westhoff, the term adminiculum was applied to what is here called aedeagus. I do not believe that his interpretation of Westhoff was correct, since the term adminiculum was used for the supportive guide of the intromittent organ and not for a part of the organ itself.
5. Alexander (1942) cites other terms used for the basistyle; they are paramere, coxite, pleurite, gonostipes and side piece.
6. The term gonapophysis is used by Byers (1961) for a process which in this paper is designated as an outpocketing of the ninth sternum located at the base of the adminiculum. Such structures are comparable to the genital palpi or parameres as recognized by Wesche (1906).

TABLE III.—Terminological Equivalents for Female Abdominal Structures.
(For notes, see end of table.)

Frommer	(Snodgrass (1903) ³)	Wesche (1906)	Berlese (1909)	Bodenheimer (1924)
1) 1st segment	1st segment	1st segment	2nd segment	2nd segment
2) 8th tergum	8th tergum		9th tergum	9th tergum
3) 8th sternum	8th sternum	8th sternum	9th sternum	9th sternum
4) Extensions of 8th sternum (= hypovalvae)	Appendages of 8th sternum	Valvula inferior, or ventral egg guide		Extensions of 9th sternum forming the "Legerohre"
5) 9th tergum	9th tergum		10th tergum	10th tergum
6) Fragment of 9th tergum?				
7) 9th sternum	9th sternum and rudimentary 2nd gonapophyses ⁴ when they occur	Lamella anterior	10th sternum and mesostyli	10th sternum
8) Vaginal apodeme, furca (Byers, 1961)	1st gonapophyses			
9) 10th tergum	10th tergum and suranal plate ⁵			11th tergum
10) 10th sternum? ¹				
11) 11th tergum ²	suranal plate			
12) Infra-anal plate = 11th sternum?	Podical plates ⁶		11th sternum	11th sternum
13) Cerci	Cerci	Valvula superior or dorsal egg guide	Cerci	Cerci

TABLE III.—Terminological Equivalents for Female Abdominal Structures.—*Concluded*
(For notes, see end of table.)

Frommer	Sellke (1936)	Rees & Ferris (1939)	Crampton (1942)
1) 1st segment	2nd segment	1st segment	1st segment
2) 8th tergum	10th tergum ⁷	8th tergum	8th tergum or epigynium
3) 8th sternum	10th sternum	8th sternum and coxopodite	8th sternum or hypogynium
4) Extensions of 8th sternum (= hypovalvae)	Ventralen Lamellen	Gonapophysis of 8th segment	Hypovalvae or hypogynal valves ¹¹
5) 9th tergum	10th tergum, but not so labelled	9th tergum	
6) Fragment of 9th tergum?			
7) 9th sternum	11th sternum (Sellke misinterpreted Bertesc)	See footnote ⁸	9th sternum processes of 9th sternum ¹²
8) Vaginal apodeme, furca (Byers, 1961)		Apodeme [below the 9th sternum and extending into the body]	See footnote ¹³
9) 10th tergum	11th tergum	10th tergum	10th tergum
10) 10th sternum? ¹		See footnote ⁹	
11) 11th tergum ²		11th tergum ¹⁰	11th tergum ¹⁴
12) Infra-anal plate = 11th sternum?		11th sternum	Bipartite plate below the anal opening ⁶
13) Cerci	Cerci	Cerci	Cerci

1. If we recognize the infra-anal plate as the true eleventh sternum then the tenth sternum is represented by a membranous area between sternum nine and eleven.
2. No evidence of an eleventh tergum was found. See discussion in text.
3. This earlier interpretation for those parts called gonapophyses is no longer maintained. Snodgrass (personal communication) now believes in a sternal rather than an appendicular origin for these parts.
4. The rudimentary second gonapophyses (Snodgrass, 1903) are two chitinous rods that arise close to the lower ends of the ninth tergum and converge posteriorly where they unite in a continuous plate. This plate is equal to sternum nine.
5. The suranal plate (Snodgrass, 1903) is equal to a distalmost, triangular tip of the tenth tergum. Crampton apparently considered it the eleventh tergum and used the term suranal, supra-anal plate or epiproct for dorsal-plates found in those instances where the tenth and eleventh segments become indistinguishably fused. The term subanal plate or hypoproct was used by Crampton for comparable ventral plates.
6. Snodgrass (1903) called the plate found below the anal opening the podical plate. Crampton (1942) believed that this plate might bear some relation to paraprocts.
7. It is clear from Sellke's words that he meant to follow Berlese's terminology; however, he misinterpreted Berlese.
8. A sclerotized portion of sternum nine is labelled gonapophysis of segment nine figured for *Limonia sciophila* (Osten Sacken) but not for *Tipula* (*Lunatipula*) *reesi* Alexander. This apparently is supposed to represent two lateral plates which are fused to each other and to the ventral surface of the ninth sternum.
9. The text states that the tenth sternum is absent in crane flies, but figure 86 (Rees and Ferris, 1939) is labelled tenth sternum. Figure 89 is labelled according to the text.
10. In *Limonia sciophila* (Osten Sacken) a fragmentum which may represent a part of the tenth tergum is labelled eleventh tergum; such a sclerite is not found in *Tipula* (*Lunatipula*) *reesi* Alexander.
11. Crampton (1942) suggested the possibility that the hypovalvae may represent the ventral valves of a true ovipositor. Since the egg-laying apparatus in Tipulidae derives from the dorsal cerci and ventral hypovalvae he felt that the term ovipositor should not be used for it. He proposed the term oviscap or oviscapula, because he felt that the two structures, although having analogous functions, were not homologous, that is, not homologous to a supposedly appendicular, orthopteroid ovipositor. Since the ovipositor of orthopteroids may still be shown, as Matsuda (1957) believes, to be sternal in origin and although this structure is of dual origin in crane flies, I prefer to follow Byers (1961) in retaining the present terminology to avoid possible additional confusion.
12. Crampton (1942) states that in some tipulids processes of the ninth sternite, which I am interpreting as sclerotized portions of the ninth sternum may represent the dorsal valves of a true ovipositor.
13. Crampton believed that the vaginal apodeme might represent fused first gonapophyses (appendicular origin of the female ovipositor).
14. Crampton (1942) figured the terminal abdominal segments of a female tipulid *Clytocosmus* in which "the cercus-bearing eleventh segment (with which the anus-bearing telson has united) is apparently represented largely by the distinct, though small sclerites at the bases of the cerci, cc." The tergal portion of the eleventh segment was further identified by an area posterior to a dotted line separating the distalmost part of a plate continuous with the tenth tergum. Rees and Ferris (1939) found a similar situation in *Limonia sciophila* (Osten Sacken) and interpreted these parts in the same way.

THE MALE

The parts of the male which are associated with the reproductive apparatus and which are for the most part heavily sclerotized are 1) the eighth sternum and its appendages when present, 2) the ninth segment (hypopygium, of authors), 3) the parameres, comprising the single basimere and two telomeres on each side, 4) the aedeagus, 5) the adminiculum, 6) the genital chamber, including the so-called genital sac, 7) the semen pump (the modified endophallus), 8) the compressor apodeme of the semen pump, 9) the immovable apodemes (two anterior and two posterior) of the semen pump, 10) the semen pump brace and its extension, when present, the brace of the ejaculatory duct. By reference to the figures, the parts listed can be identified.

PARAMERES AND AEDEAGUS

The parameres in tipuline crane flies probably develop in the sternal portions of the intersegmental membrane between segments nine and ten. In the adult they are divided into two primary parts, the proximal basimere and the distal telomere. Furthermore, in crane flies the telomere is divided again into the outer and inner telomeres. The actual protrusive, or intromittent organ has been called the aedeagus by Snodgrass (1957). There is evidence that in some crane flies the sclerotized portion of the protrusive organ actually sheaths an inner flexible tube which may be endophallic in origin. According to Snodgrass (1957), the aedeagus and parameres develop from a pair of phallic lobes which divide at first into secondary lobes or phallomeres, the inner pair called mesomeres, the outer pair called parameres. The mesomeres then become hollowed on their opposed surfaces and unite with each other to form a tubular, median organ, the aedeagus. In dissecting the intromittent organ of *Dolichopeza tridenticulata* and *Dolichopeza carolus* I have noticed within this fine sclerotized outer tube still another tube. The inner tube is able to withstand the action of potassium hydroxide. At first it appeared only as a hyaline tube concealed by the more sclerotized portion of the aedeagus and visible only after its rupture; later I examined specimens in which this innermost tube projected from the tip of the aedeagus. While this inner tube may represent an aedeagus, ensheathed by a sclerotized thecal covering, it is more likely an extension of the endophallus. I have in one instance removed this inner tube and observed it with the phase contrast microscope (at 1164 \times), and it appeared

to be a double cylinder. Snodgrass (1935, p. 590, Fig. E) figures an intromittent organ which is in essence comparable to that of *Dolichopeza*. In other crane flies studied I have not been able to demonstrate this inner tube. It is possible that in these crane flies the inner tube has become inseparably connected to the inner wall of the sclerotized intromittent organ. It is equally possible that in these species the endophallus is not extended. The entire intromittent organ in the majority of crane flies studied, while quite strong and flexible, is of a very small bore; this may account for the difficulty in distinguishing the inner from the outer tubes.

The recent investigations of Neumann (1958) with *Tipula oleracea*, in which microtome sections were studied, do not show the development of such an inner endophallic tube.

It is impossible to overstress the need for abundant comparative material in a morphological study such as this. The inner tube found in *Dolichopeza* may be present within the aedeagus of *Tipula* (*Yamatotipula*) *jacobus*. In the European crane flies studied by Westhoff (1882) this may also be the case. The figures given by Westhoff (Figs. 50, 59, 60, 61) for *Tipula hortulana* Meigen, *Tipula sinuata* Fabricius, *Tipula winnertzi* Egger and *Tipula varipennis* Meigen show a structure at the extreme tip of the aedeagus (penis, of authors) which resembles that of *Dolichopeza* and *Tipula jacobus*. Westhoff stated that this structure, designated as an "austulpbaren Eichel" (= glans), had already been described by Dufour (1851) for *Tipula oleracea* Linnaeus. The glans as described by Westhoff may take various shapes. It may be drawn out to a fine point as in *Tipula oleracea* Linnaeus; in *Tipula sinuata* Fabricius it is less fine and less drawn out; and in *Tipula varipennis* Meigen and *Tipula hortulana* Meigen it is long and blunt. In the last two it is characterized by possessing a ring of fine grooves. These ring-like grooves may serve to secure the aedeagus within the bursa copulatrix. This information supports the contention that an inner tube exists within what has been called the penis. While the terms theca and endotheca could be used for the sclerotized parts of the intromittent organ of *Dolichopeza*, such use is arbitrary and only suggests one possible ontogenetic explanation for the final structure of the intromittent organ. It would be just as easy and perhaps preferable to visualize the theca and endotheca as comparable to the aedeagus and endophallus (Snodgrass, 1957) and the innermost tube as merely an extension of the endophallus. Text figure 1 indicates these supposed relation-

ships in diagrammatic form. Until ontogenetic studies of development of the reproductive system in crane flies are made, a final decision concerning the homologies of these parts must be deferred.

In the Tipulinae the parameres are found in one of two primary positions. In the first type the basimere is completely free from the ninth sternum as in *Brachypremna* and *Megistocera*, and in the second it is either partially or wholly fused with the ninth sternum as in *Tipula* (*Lunatipula*) *triplex* Walker (Figs. 6, 9, 10).

In order to give correct morphological names to the parts comprising the intromittent organ and semen pump it would be necessary to know the exact manner in which these parts have developed. Since this is not yet known for the Tipulidae a flexible terminology for the component parts is given.

Following Snodgrass (1957) we may assume that the aedeagus is formed from fused mesomeres. The two alternatives following aedeagus formation are, 1) formation of a sheath around the aedeagus and 2) enlargement of the endophallus. Figure a of text figure 1 diagrammatically portrays the intromittent organ after fusion of mesomeral lobes. At this point we find the aedeagus (Ae) and, within, the endophallus (Enph 1). Note the connection of endophallus and ejaculatory duct (ED). In Figure b the endophallus (Enph 1) has enlarged to form an extension, labelled (Enph 2), which forms a second tube within the first of figure a. The inner portion of this endophallic extension is cross-hatched in the figure. In figure c the inner layer of the endophallus is not cross-hatched, but the organ is at the same stage as in figure b. Figure d shows the specialization of endophallus to produce the bulb of the semen pump and is labelled (Enph 1). Figure e gives a schematic representation of the semen pump and intromittent organ. The cross-hatched area (X), of this figure represents the site of the compressor apodeme. Note that the aedeagus (Ae) is continuous with the membranous sac at the base of the bulb. The base of the membranous sac while not labelled is represented by the stippled ring of tissue at the base of the semen pump. Figure f is a transverse section of the semen pump and the compressor apodeme (CA).

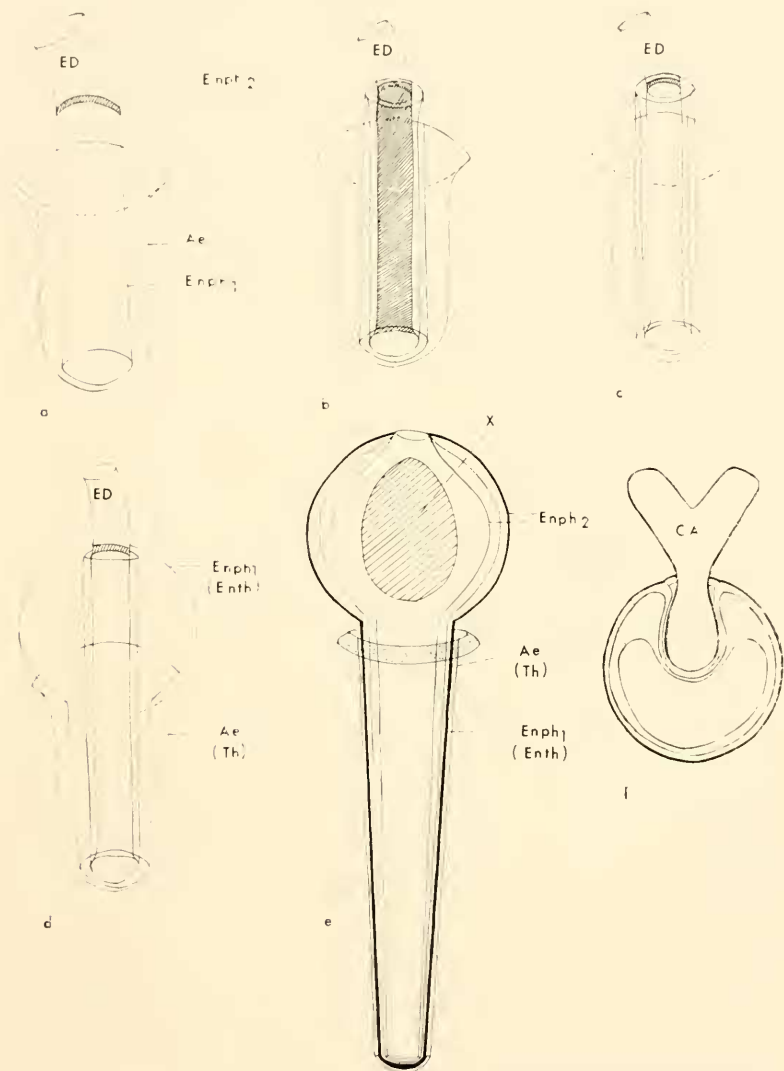
These figures as just explained give the terminology which should be used in the case where enlargement of the endophallus can be shown to have taken place. Such a situation seems to obtain in *Dolichopeza*.

If it can be demonstrated that a thecal sheath forms about an aedeagus and that endophallic enlargement does not occur, then

what was called aedeagus should be called theca (Th) and what was called endophallus should be called endotheca (Enth).

The aedeagus would then be what was called endophallus two (Enph 2) and within it an endophallus (not labelled).

The presence of an inner tube within the sclerotized intromittent organ has not been demonstrated for species other than those in



TEXT FIGURE 1.—A schematic and hypothetical representation of the development of the intromittent organ and the semen pump in the Tipulinae.

the genus *Dolichopeza*. If the reader ignores those parts of the figures showing the endophallic enlargement, no difficulty should be had in visualizing the development in all the other Tipulinae.

ADMINICULUM

Caudally, in the median line, there is a strengthened portion of the intersegmental membrane between segments eight and nine, the adminiculum (Figs. 10, 11, 12). This structure serves as a support and guide for the intromittent organ. It is continuous with the ventral wall of the genital chamber and is equipped with muscles extending anteriorly to the antecosta of the ninth sternum. By contraction of these muscles the adminiculum is drawn toward the ninth tergum.

The adminiculum is usually most conspicuously developed in its median portion, although it may have on either side various prongs or arms; these arms may be free or may lie in the walls of the genital chamber. The lateral arms and the median body do not represent gonapophyses (Snodgrass, 1904) but are merely sclerotized portions of the intersegmental membrane. The thickenings of the genital chamber extending anteriorly from the adminiculum have been called adminicular rods (Byers, 1961). Such thickenings may be seen in the genus *Dolichopeza* and in *Tipula* (*Nobilotipula*) *nobilis*. Adminicular rods seem to support the walls of the genital sac and, in the case of *Dolichopeza* and *Tipula* (*Nobilotipula*) *nobilis* where they extend to the semen pump, serve as a fulcrum upon which the semen pump rotates (Fig. 41). The adminiculum can be observed to assume many shapes providing excellent characters for the systematist (Byers, 1961).

Loew (1873) believed the adminiculum was the actual intromittent organ and applied to it the term "Copulationsglied."

GENITAL CHAMBER AND GENITAL SAC

The genital chamber is formed by an invagination of the intersegmental membrane between the ninth and tenth segments. The thin walls of this chamber are concealed within the abdominal segments, and it is usually found as in *Tipula* (*Lumatipula*) *triplex* within the ninth segment; however, when the intromittent organ becomes greatly lengthened as in *Tipula* (*Trichotipula*) *macrophallus*, a slender portion of the genital chamber may extend forward well into the thorax. The term genital sac has been used for the walls of this chamber. The intromittent organ is found within the chamber and when it is withdrawn becomes bowed, its elasticity

causing the walls of the chamber to become taut (Text Fig. 2). The aedeagus and the wall of the genital chamber are contiguous at the base of the aedeagus (Text Figs. 3a, b). The dorsal wall of the genital chamber may also be sclerotized to a greater or lesser extent, and it is to such a sclerotization that Rees and Ferris (1939) gave the name epimere. This sclerotization takes various forms, for example a transverse bar in *Tipula (Vestiplex) fultonensis*, and a broad Y-shaped sclerotization (epimere) in *Tipula (Lunatipula) triplex*; alternatively the sclerotization may be absent, as in the genus *Dolichopeza*.

Dufour misinterpreted the true nature of the genital sac, as he thought it was fused to the intromittent organ. It is clear, however, that the intromittent organ is so fused only at its base where the semen pump develops.

SEMIEN PUMP AND COMPRESSOR APODEME

The semen pump (Text Figs. 1, 3) is derived from a specialized portion of the endophallus which is bulblike. Its wall is invaginated at one point, and in this invagination is found a movable apodeme, the compressor apodeme, so called by virtue of its function. This apodeme has been called the piston apodeme by Abul-Nasr (1950) and the ejaculatory apodeme by Wesche (1906). Keuchenius (1913) was unable to interpret the finer detail of this structure. I have been able to dissect it under the binocular microscope and observe it at 100 \times magnification. Within the bulb are found a number of membranes. At the position where it is invaginated, the hardened wall of the pump gives way to a flexible membrane which allows the compressor apodeme to make its movements. The outer wall of the endophallic enlargement arises from a point caudal (morphologically anterior) to the compressor apodeme at the connection of the ejaculatory duct and runs through the body of the semen pump out through the intromittent organ then invaginates and retraces its path into the pump, finally making connection with the ductus ejaculatorius. (See Text Fig. 1, where the probable derivations of the parts of the intromittent organ are indicated diagrammatically; compare the schematic drawings of the semen pump and intromittent organ in Text Figs. 1e and 3a.)

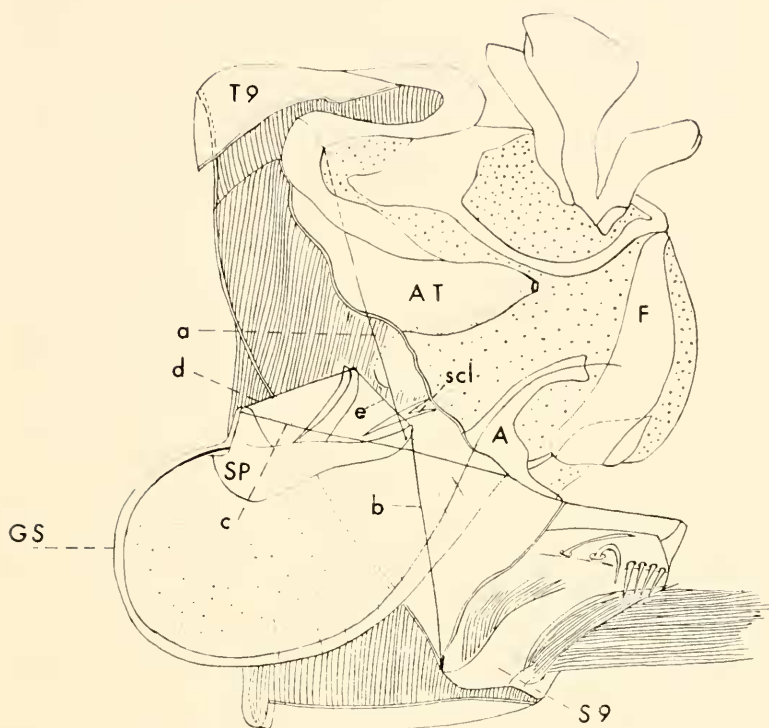
Whether the compressor apodeme is derived from the wall of the semen pump (endophallus) or from some other source, as proposed by Abul-Nasr (1950) for the anisopodid, *Anisopus fenestralis*, is a question which cannot be resolved until a study of its ontogenetic development is made.

IMMOVABLE APODEMES OF THE SEMEN PUMP

If one dissects out the semen pump of a crane fly, there can be observed in addition to the aforementioned compressor apodeme four other apodemes. These envelop the body of the pump and serve for the attachment of muscles on both sides of the compressor apodeme, enabling this apodeme to make its movements. In addition, there are three sets of muscles attached to the immovable apodemes which serve to rotate the semen pump (Text Fig. 2). From each of the arms of the anterior immovable apodemes the first set of these muscles extends to either side of the base of the adminiculum, and by their contraction the semen pump rotates in the sagittal plane, resulting in a caudal extension of the intromittent organ. From each of the arms of the immovable posterior apodemes the second and third set of muscles arise. The first set extends to the antecosta of the ninth sternum and upon contraction the semen pump rotates in the sagittal plane, withdrawing the intromittent organ into the genital chamber. The second set of muscles extends to the dorsalmost edge of the ninth sternum, where it joins the ninth tergum. Contraction of these muscles causes the semen pump to rotate in the sagittal plane resulting in a caudal extension of the intromittent organ (Text Fig. 2). The immovable apodemes are developed from a portion of the dorsal wall of the genital chamber, which envelops the body of the semen pump.

The semen pump (pompetta, Abul-Nasr, 1950), compressor apodeme (piston apodeme, Abul-Nasr, 1950), immovable apodemes and intromittent organ (penis, Abul-Nasr, 1950) of a crane fly such as *Tipula* (*Lunatipula*) *triplex* bear a striking resemblance to similar structures in the anisopodid figured by Abul-Nasr (1950). If these structures are to be thought of as homologous, as is suggested by their similarity in form, location, and probable function, then certain differences in the interpretation of the parts become evident.

Abul-Nasr (1950, p. 376) states that the penis "is composed of a filamentous cuticular tube which is devoid of cellular coat except at its most proximal part, where the penis tube is surrounded by the pompetta." He makes no mention anywhere in his paper of an inner tube, such as occurs in the genus *Dolichopeza*. The anisopodid which he studied is a very small fly, and it seems that if such an inner tube exists in this fly it could easily have been overlooked, especially when we consider the difficulty encountered in locating it in *Tipula*.



TEXT FIGURE 2.—Semidiagrammatic parasagittal view of the terminal abdominal segments of a male crane fly drawn to show muscle attachments necessary for the movements of the semen pump, compressor apodeme, and intramittent organ. Muscles (d) and (e) move the compressor apodeme: contraction of muscle (d) compresses the lumen of the semen pump expelling semen while at the same time the "heel" of the compressor apodeme within the pump closes the opening into it from the ejaculatory duct; contraction of muscle (e) reopens the entrance into the semen pump and causes a partial vacuum which can draw additional semen into the bulb of the pump. Muscles (a), (b), and (c) are concerned with rotation of the semen pump resulting in movements of the intramittent organ: contraction of (a) and (c) results in a counter-clockwise movement of the semen pump and eversion of the intramittent organ; contraction of (b) results in a clockwise rotation of the semen pump and retraction of the intramittent organ. d = muscles from compressor apodeme to anterior immovable apodeme; e = muscles from compressor apodeme to posterior immovable apodeme; a = muscle from posterior immovable apodeme to the dorsalmost part of sternum nine where it meets the ninth tergum. b = muscle from posterior immovable apodeme to the antecosta of sternum nine. c = muscle from anterior immovable apodeme to base of adminiculum; AT = anal tubercle; A = adminiculum; F = fragmentum of sternum nine; SP = semen pump; scl = sclerite in dorsal wall of genital chamber (epimere, Rees and Ferris, 1939); GS = genital sac. (Redrawn and modified from Rees and Ferris, 1939.)

Then again, the semen pump and associated structures may not develop in the same way in tipulines and anisopodids. Aside from the invaginated portion of the semen pump (thin elastic tissue, Abul-Nasr, 1950) which enables the movement of the compressor apodeme, Abul-Nasr makes no mention of any other membranes within the body of the pump itself, although his figure (p. 370) suggests some others. He states that the piston apodeme "springs from a large cuticular structure in the shape of a bird's sternum without a keel." He goes on to say that this structure "serves as a hood over the pompetta and provides a suitable surface for the attachment of muscles responsible for the movements of the piston." Unfortunately I have not been able to understand fully his explanation of the derivation of the pompetta and the piston apodeme. His figures leave something to be desired. Nevertheless, no such hood occurs in the Tipulinae, and the muscles which work the compressor apodeme extend to the immovable apodemes. Further, Abul-Nasr describes the semen pump as a "small cuticular box with two lateral alate apodemes." He does not make it clear whether these apodemes arise as outgrowths of the pompetta itself or are, as I believe occurs in the Tipulinae, developed from cuticular thickenings of the dorsal wall of the genital chamber.

In the work of Wesche (1906) we find a discussion concerning movements of the semen pump and the intromittent organ. Wesche's figure (Plate 24, Figure 24) is reproduced upside down, and in addition his Figure 26 is both crudely and improperly drawn, failing to show the anterior immovable apodemes and showing the compressor apodeme at a right angle to its normal position at rest. Muscles are figured attached to this apodeme; however, their origins are not diagrammed. The median portion of the adminiculum is termed "theca" while portions of the lateral arms of this body are called the "apodemes of the penis, the double apodeme, the great apodeme, and the forcipes interiores."

A consideration of Wesche's paper convinces me that he only partially understood the working mechanism of the semen pump and the movements of the intromittent organ. Since he made his observations from materials placed on slides, it is easy to see how he could have drawn improper conclusions and figured the parts incorrectly.

Bodenheimer (1924) criticized Wesche's interpretation concerning the mechanics of the semen pump and offered his own observations. He pointed out that Wesche ascribed great importance to the compressor apodeme, which, as Bodenheimer interprets Wesche,

causes a rotation of the semen pump and is thereby able to open and close its opening. Bodenheimer believed that such a function (probably referring to the opening and closing of the lumen of the semen pump) is carried out by smooth or striated musculature and not by skeletal parts. Hence it can be seen that it did not occur to Bodenheimer that the compressor apodeme could actually close the opening into the semen pump. In an earlier section (p. 409) of his paper, Bodenheimer criticizes Westhoff's (1882) idea that the semen pump is a depot for the storage of sperm and states that its vesicular inflation ("blasige Auftreibung") is more likely due to the action of the numerous muscles which are attached to it. Though Bodenheimer granted that the semen pump might have a temporary storage function during copulation, he thought even this unlikely. It seems that Bodenheimer attributed a semen pumping function to this structure, but he does not state this outright. He attributes the outward protrusion of the intromittent organ to the concerted action of the so-called "Muskelpresse" of the posterior abdomen. Whether he recognized the function of the muscles of the immovable apodemes which rotate the semen pump cannot be determined.

The semen pump is given support from the rear by a small median brace (Figures 48, 53) which runs from the bulb of the semen pump at the level of the entrance of the ductus ejaculatorius to the innermost posterior margin of the sheath of the pump. This brace lies in the mid-line, between the posterior immovable apodemes. Its length varies in different species and is in some quite short. In these latter species the enveloping sheath of the pump is of necessity snugly fit around the semen pump, but in species where the brace is long one can see a distinct separation between semen pump and sheath. This seems to be a point worth stressing since when the brace is short and the sheath close-fitting, the apodemes which develop from this sheath may appear to be formed from the body of the pump. The study of many different species has, however, made this relationship clear.

At times the brace is continued up along the posterior (morphologically dorsal) surface of the ejaculatory duct at the point of its union with the semen pump. I have called this extension the brace of the ejaculatory duct (Figures 51, 52, 53); however, it does not seem to have an independent derivation.

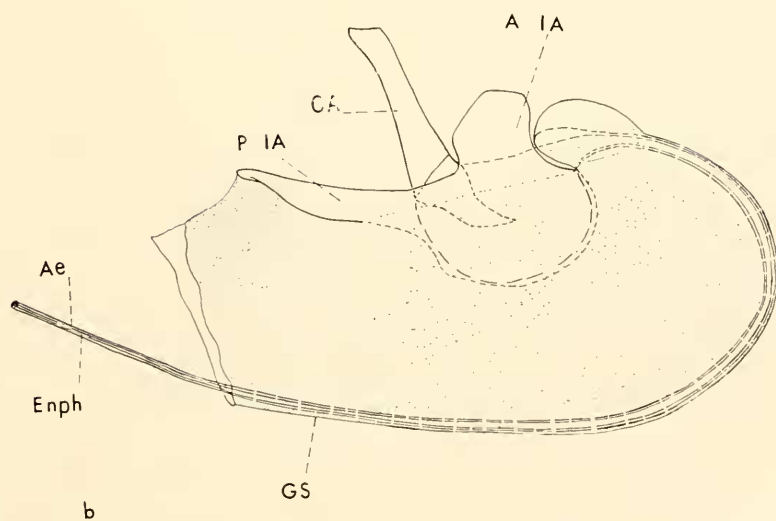
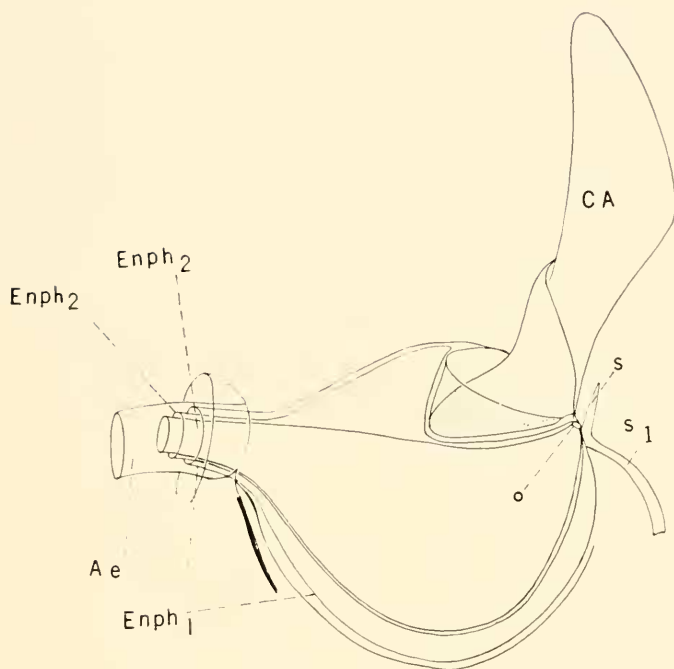
TYPES OF SEMEN PUMP—INTROMITTENT ORGAN COMPLEX

Three distinct types of arrangements of the semen pump and intromittent organ may be observed in the tipuline crane flies studied:

TEXT FIGURE 3

TEXT FIGURE 3.—FIG. a.—Schematic drawing of semen pump and compressor apodeme in a crane fly such as *Dolichopeza*. In species other than those of the genus *Dolichopeza* the presence of an endophallic enlargement (Enph₂) within the tube-like intromittent organ (Ae and Enph₁) could not be definitely established. Gross dissection of the body of the semen pump of species in the genus *Tipula* did suggest the development of an endophallic enlargement; however, figures (Neumann, 1958) of sagittal sections of the semen pump of *Tipula paludosa* do not show any development of the endophallus. Note the sclerotized bar (S₁) from the median line of the posterior apodeme (not figured) extending to the semen pump (O) where the pump joins the ejaculatory duct; and the brace of the semen pump, a sclerotized bar (S) which is a continuation of S₁. CA = compressor apodeme; Ae = aedeagus; Enph = endophallus; Enph₂ = endophallic enlargement. FIG. b.—Schematic drawing of semen pump and associated structures. Note: 1) the figure does not show any endophallic extension. PIA = posterior immovable apodeme; AIA = anterior immovable apodeme; GS = genital sac.

TEXT FIGURE 3



Type I—Intromittent organ arises as an unbowed extension of the semen pump. Examples of this type are *Brachyremna dispellens* (Figs. 6, 51, 52) and *Megistocera longipennis*.

Type II—Intromittent organ only slightly bowed. Anterior immovable apodemes much enlarged and united along their median basal line but slightly separated distally. A second pair of apodeme-like structures (I have only seen cleared specimens of this and am unable to say whether muscles are attached to these processes in the living fly) is found lateral to the semen pump. The basal portion of the aedeagus is specialized into an elongate and somewhat club-shaped process. This type has been found in only one fly of all those studied, *Tipula (Nippotipula) abdominalis* (Figs. 1, 7).

Type III—This form is by far the most common and was found in all other flies studied (Text Figure 3b). In this type the intromittent organ is strongly bowed, and among the species studied this condition finds its greatest expression in the genus *Nephrotoma* and in *Tipula (Trichotipula) macrophallus*, in which the intromittent organ extends anteriorly from the semen pump in the longitudinal axis of the body, makes a short arc, and then continues back towards the terminal abdominal segments.

TORSION: TEMPORARY AND PERMANENT

Sellke (1936) describes what might be called a temporary torsion of the male terminal segments during copulation. After copulation these segments return to their normal positions.

No good evidence of permanent torsion (rotary inversion or "transinversion" in the sense of Crampton 1942) has been seen in any of the crane flies studied except *Brachyremna dispellens* and *Megistocera longipennis*. I have been able to study only two specimens of the former and one of the latter, and in all these the ninth segment appeared to have rotated while the tergum and sternum of segment eight were only partially rotated (about 90°). Dr. C. P. Alexander (personal communication) has examined additional specimens and states that the rotation does not seem to be complete, that is, 180°. In *Brachyremna* and *Megistocera* the anal tubercle was observed to be in a ventral position and the adminiculum in a dorsal position. The internal organs of these dried specimens had already disintegrated, hence I could find no evidence of a looping up of the ejaculatory duct from left to right over the top of the hindgut. Crampton (1942: 87) refers to the work of Edwards (1924), who described a permanent torsion in the tipulid

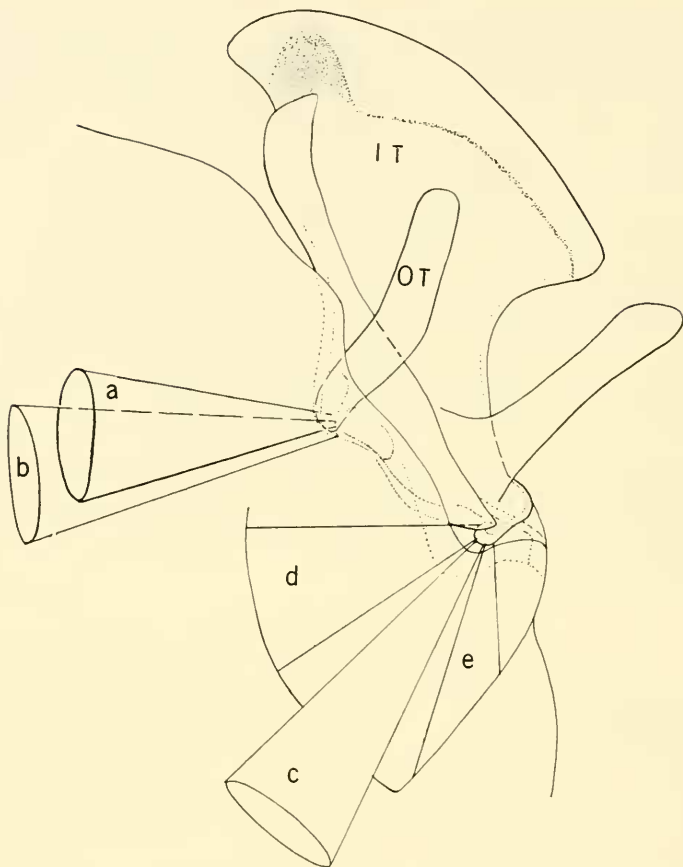
Styringomyia and knew of only two other cases of complete and permanent torsion in the Tipulidae, occurring in the genera *Molophilus* and *Amphineurus*. He mentioned in addition a case of incomplete torsion in the genus *Micromastix* (probably a synonym of *Longurio*).

Abul-Nasr (1950) discusses torsion in an anisopodid. The relative positions in the adult anisopodid, save the anal tubercle, are similar to those found in an adult crane fly such as *Tipula*, the major difference being only in the position of the anal tubercle, which in the anisopodid adult is ventral but which in the adult tipulid remains dorsal. By comparing the tipulid with the anisopodid I can see no visible evidence of any torsion in the adult crane fly other than the position of the ductus ejaculatorius relative to the compressor apodeme. One possible explanation for this phenomenon is that if the endophallus alone were to make a rotation of 180° in the development of the fly the unchanged position of the anal tubercle would be explained. Here again developmental studies may elucidate the situation.

ORIGIN OF THE TELOMERES

We have already considered the development of the parameres and discussed their division into two primary parts, the basimere and telomere. Workers have in the past attributed the origin of these parts to appendages of the genital segments. As a result of such thinking, names such as coxopodite and gonocoxopodite have been given to the structure here recognized as the basimere. Matsuda (1958) gives a history of the problem concerning the origin of male genitalia.

A dissection of the ninth abdominal segment reveals the origins and insertions of the various muscles which move the two telomeres. From both the basimere and the antecosta of the ninth sternum (Text Figure 4) muscles extend to the inner telomere. If the basimeres were of appendicular origin, one might expect muscles which operate the telomere to spring from the basimere alone; on the other hand if the parameres are intersegmental in origin, we might expect muscles which run to them to arise at the antecosta of the ninth sternum, and then, with the secondary divisions of the parameres, muscles might run to the basimere as well. Because other workers have indicated movement of muscle attachments, it is difficult to arrive at any final decision concerning this argument. In other words muscle attachments may not be the best criterion for settling this problem.



TEXT FIGURE 4.—Telomeres of *Tipula* (*L.*) *triplex*, male. OT = outer telomere; IT = inner telomere; (a) = muscle from outer telomere to antecosta of the ninth sternum; (b) = muscle from inner telomere to antecosta of the ninth sternum; (c) = muscle from inner telomere to antecosta of the ninth sternum; (d) and (e) muscles from the inner telomere to the rim of the basimere.

ANAL TUBERCLE OF THE MALE

In the male fly the last distinctly recognizable segment is the ninth. There is, however, a fleshy tubercle at the apex of which opens the alimentary canal. In some flies studied, this tubercle appears sclerotized both dorsally and laterally, in some only laterally. Berlese (1909) figured such plates and considered them as evidence of an eleventh tergum. This of course is due to his idea that the first abdominal segment was lost in the crane flies. It would appear as if Berlese, trying to identify the basic eleven abdominal segments, started his count from the rear. In any case no distinct separation

into tenth and eleventh segments is visible. In keeping with the line of reasoning which is proposed for these segments in the female, one might imagine a decrease in sclerotization of the tenth and eleventh segments with reduction in size. Because we can as yet come to no definite conclusion concerning the nature of these segments in males I have called this structure the anal tubercle and assigned it tentatively to segments ten and eleven. Whether the sclerotizations in the wall of the tubercle are tergal elements (of either or both segments) or merely secondary in nature cannot as yet be decided.

GROSS INTERNAL ANATOMY OF THE MALE REPRODUCTIVE SYSTEM

The gross internal anatomy of the remaining parts of the male reproductive system is represented in Figures 47, 50, 55-58, 91. The parts of this portion of the system are as follows: 1) a pair of testes, 2) a pair of vasa deferentia, 3) the seminal vesicle, 4) a pair of accessory glands, 5) the ejaculatory duct and a vesicular gland at the distal end of the ejaculatory duct.

Table IV shows the terminology used by various workers who have studied the tipuline reproductive system.

A comparison of my Figures 55 and 56 with those of Dufour (1851) and Keuchenius (1913) shows that the vasa deferentia may or may not be swollen at some point along their lengths. Although I have made no histological studies of these parts, the descriptions by Keuchenius (1913) and Bodenheimer (1924) seem to agree with my observations, the only departure being the possible lack of a swollen portion along the length of the vasa deferentia. Since these other workers studied but one species (*Tipula oleracea*) they could of course not see such variation. In a freshly-dissected fly, it is readily observed that the vasa deferentia come close together at some point and from there on run side by side as one, coiling in some flies. They have not been found to fuse with each other in any of the flies studied, although Byers (1961) believed this occurred in *Dolichopeza polita*. In specimens of *Dolichopeza tridenticulata* it seems to me that they are separate as in all other Tipulinae examined. Because they are very close to each other and because each is enveloped by a muscle coat which is further covered by a layer of fatty tissue (tunica adipo membranacea, Keuchenius, 1913) this separation is not readily noticed. Table V gives the results of observations of these parts. Another variation that may readily be observed is the degree of coiling of the ejaculatory duct.

TABLE IV.—Terminological Equivalents for Male.

INTERNAL REPRODUCTIVE ORGANS				
Frommer		Dufour (1851)	Keuchenius (1913)	Bodenheimer (1924)
1.	Testes	Testes	Testes	Testes
2.	Vas deferens	Vas efferens Vesicula seminalis Vas deferens	Vas deferens	Vas efferens Vesicula seminalis Vas deferens
3.	Seminal vesicle	Bladdery widening which forms the commencement of the ductus ejaculatorius	Bladdery widening which forms the commencement of the ductus ejaculatorius	Bladdery widening which forms the commencement of the ductus ejaculatorius
4.	Ductus ejaculatorius (seminal duct, Byers, 1961)	Ductus ejaculatorius	Ductus ejaculatorius	Ductus ejaculatorius
5.	Accessory glands	Accessory glands	Accessory tubes	Abdominale Drüsen
6.	Vesicular gland (Byers, 1961)			

TABLE V.—Nature of the vas deferens and ejaculatory duct in some representative crane flies.

SPECIES STUDIED	Vas deferens	Ejaculatory duct
<i>Dolichopeza (Oropeza) tridenticulata</i>	not swollen	loosely coiled
<i>Dolichopeza (Oropeza) carolus</i>	not swollen	loosely coiled
<i>Prionocera oregonica</i>	swollen	uncoiled
<i>Tipula (Orcomyza) latipennis</i>	swollen	uncoiled
<i>Tipula (Vestiplex) fultoneusis</i>	swollen	closely coiled
<i>Tipula (Lunatipula) triplex</i>	not swollen	closely coiled
<i>Tipula (Lunatipula) bicornis</i>	not swollen	closely coiled
<i>Tipula (Hesperotipula) tryptophora</i>	swollen	closely coiled
<i>Holorusia (Holorusia) grandis</i>	not swollen	twisted but not into a helix
<i>Tipula (Yamatotipula) furca</i>	swollen	uncoiled
<i>Tipula (Trichotipula) orozeoides</i>	swollen	loosely coiled
<i>Nephrotoma eueeroides</i>	swollen	uncoiled
<i>Nephrotoma ferruginea</i>	swollen	uncoiled

At the base of the semen pump and arising as an extension of the epithelium of the ejaculatory duct is a vesicular gland (Figs. 47, 50). This gland is variable in size, but it was found in all the flies studied. The muscles which move the compressor apodeme may conceal portions of this gland, and when this occurs the gland appears as if it were two glands, one at each side of the semen pump (vesicular glands, Byers, 1961). Removal of the muscles that extend from the compressor apodeme to the anterior and posterior immovable apodemes, makes possible the observation that the gland is single and surrounds the compressor apodeme in a ring-like fashion. Byers (1961) figures this gland (for the first time) as it occurs in *Dolichopeza*, in which genus it is most well developed. Here it becomes swollen into two bodies, whose shape resembles that of lima beans, one at either side of the semen pump. Byers (1961) has shown that the epithelium of this organ is composed of longitudinal bands of flattened, hexagonal cells.

Histological studies of the male reproductive system in crane flies have been made by Dufour (1851), Cholodkovsky (1905), Keuchenius (1913) and Bodenheimer (1924).

THE FEMALE REPRODUCTIVE SYSTEM

The female tipuline shows much less differentiation in the genital segments than does the male. The parts of the female associated with the reproductive apparatus, which are for the most part heavily sclerotized, are 1) the eighth sternum with its extensions, the hypovalvae, 2) the ninth tergum, 3) the ninth sternum, 4) the vaginal apodeme, 5) the tenth tergum, 6) the infra-anal plate (eleventh sternum?), and 7) the cerci. For a generalized diagram of the parts now to be considered see Fig. 59. The eighth abdominal segment shows modification only in the eighth sternum and it will be considered first.

EIGHTH STERNUM

Projecting from the distal end of the eighth sternum are the blade-like hypovalvae, which are here considered extensions of the eighth sternum that function in oviposition. They are variable, being developed and elongate, as in *Tipula (Lumatipula) triplex*, to very small or rudimentary, as in *Tipula (Vestiplex) spp.*

Rees and Ferris (1939) designate the basal area of the eighth sternum "8th sternite and coxopodite," while each hypovalve is labelled "gonapophysis of the 8th segment." They state that from the posterior dorsal angle of the eighth sternum in *Limonia sciophila*, a limoniine crane fly, there arises an elongated, bladelike lobe, the base of which is partially set off by a deep furrow from the remainder of the sternum, although there is no actual separation of the parts. They adopt the view that this lobe represents a gonapophysis (in the appendicular sense of the term). As I do not consider this structure a gonapophysis but rather a modified portion of the sternal region and because this term has had too many meanings, I have avoided the term gonapophysis. The term hypovalve has shortcomings as well. In female Diptera the hypovalve (hypogynal valve, Crampton, 1942) is defined as an appendage of the eighth sternum homologized with the gonapophysis. I have used it in order to avoid adding yet another term to the already replete terminology for this part and because the term is certainly more restricted in meaning than is gonapophysis.

NINTH TERGUM

The ninth tergum undergoes no special modification in any of the flies I have studied. Rees and Ferris (1939:72, Fig. 87) figure what I believe is probably a separated piece of the ninth tergum. They called this sclerite "coxopodite."

NINTH STERNUM

Directly below the ninth tergum and above the hypovalvae is a roughly triangular-shaped extension of the body wall, the ninth sternum. It is not always entirely sclerotized, and even when it is the actual limits of the sclerotized areas are not always distinct. In some flies, such as species of the genus *Dolichopeza*, a sclerotized extension from the ninth tergum runs down to meet the heavily sclerotized portions of the ninth sternum. The ninth sternum may vary in shape and size and in many instances offers good taxonomic characters. Portions of the sclerotized areas of the ninth sternum have been considered gonapophyses; again I believe this term unwarranted.

VAGINAL APODEME

The term vaginal apodeme of the female has been used by dipterists (Tuxen, 1956) for sclerotizations in the vaginal wall in Nematocera. In the literature concerning the Phlebotominae (Diptera:Psychodidae) a structure in the same general area as this apodeme has been called the furca. Byers (1961) adopted this term furca for what I recognize as the vaginal apodeme because in flies of the genus *Dolichopeza* it is forked. In many tipulines I have examined this structure is not forked. Snodgrass (1903) believed that a plate, which apparently separated from the apodeme proper in *Tipula vittata*, might represent the fused first gonapophyses, but I do not think this plate represents fused gonapophyses.

The apodeme is found in a usually membranous area of the eighth sternum caudal to the gonopore and projects into the body of the fly, where it is found lying directly above the common oviduct. It is not equipped with muscles of any sort, as far as I can tell.

TENTH AND ELEVENTH TERGA, INFRA-ANAL PLATE
(ELEVENTH STERNUM?) AND CERCI

The most conspicuous modification in the tenth segment and more specifically the tenth tergum is a median longitudinal inflection (Figs. 68, 69, 71) to which powerful muscles that move the cerci

are attached. In addition there are intersegmental muscles which take their origin from the ninth antecosta, extend through segment ten, and insert on the rim of the cercus, as well as muscles that originate on the tenth antecosta and insert on the strongly sclerotized base of the cercus. Rees and Ferris (1939) called attention to a sclerite found in *Limonia sciophila*, located posterolaterally to the tenth tergum and basal to the cercus. In that species they showed that muscles arise from the tenth antecosta and insert on this sclerite, which was thought to represent a fragmentum of the eleventh tergum.

As evidence for the supposed homology of this sclerite with a fragmentum of the eleventh tergum Rees and Ferris called attention to a similar sclerite found in *Gryllus*, which was discussed by Snodgrass (1933:70). I feel that the comparison with the gryllid is unjustified; however, the sclerite may truly represent a part of the eleventh tergum in the limoniine. Rees and Ferris stated that no such sclerite is found in *Tipula reesi*, nor did I find it present in any Tipulinae.

It is possible that the muscles which operate the cerci and arise from the tenth antecosta are true intersegmental muscles. The muscles that arise from the ninth antecosta as well as those which arise from the median longitudinal inflection of the tenth tergum may represent secondary adaptations for the operation of the cerci in oviposition. Similar secondary modifications have apparently occurred in the Japygidae (Diplura), where the muscles which operate the pincers-like cerci occupy the greater portion of the tenth abdominal segment. I am inclined to believe that in the species I have studied no true eleventh tergum is present and that only the infra-anal plate, lying directly below the anus, appearing as a flap-like appendage which is often divided into two, may represent the eleventh sternum. No sclerotized tenth sternal plate can be found in female crane flies. The membranous connection between the infra-anal plate and the ninth sternum may be thought of as the region of the tenth sternum.

The cerci arise at the apex of the tenth tergum and usually appear as strong blade-like elements but may be reduced to fleshy lobes, as in *Tipula bicornis*, *Tipula (Hesperotipula)* spp., and *Tipula nobilis*.

INTERNAL ANATOMY OF THE FEMALE REPRODUCTIVE SYSTEM

The remaining parts of the female reproductive system consist of the following: 1) a pair of ovaries, 2) the common oviduct, 3) the lateral glands of the common oviduct, 4) the bursa copulatrix

and three spermathecae with their respective ducts, 5) a pair of accessory glands, and 6) the genital chamber (Figs. 42, 59, 86, 89).

Because these parts of the female genital tract bear great similarity to those of the chironomid described by Abul-Nasr (1950), I believe that in all probability they have arisen in the same fashion. There are, however, noticeable differences which must be pointed out.

Perhaps the most significant difference is the presence of the already described ninth sternum, which is well developed in the tipulid and rudimentary in the adult chironomid. No structure comparable to the "insula" (in the sense of Abul-Nasr) of the chironomid occurs. Therefore we see no flap-like evagination between the openings of the bursa copulatrix and the opening of the accessory glands when these openings are separate from each other.

GENITAL CHAMBER

If we accept Abul-Nasr's (1950) interpretation of the development of the chironomid, and if it is actually comparable to that of the tipulid, then the genital chamber of the crane fly is comparable in extent to what he has designated the atrium (vaginal and caecal portions considered as one). The genital chamber occupies the interspace between the eighth and ninth sterna. Because of the absence of "insula," no distinct division of the genital chamber into caecal (accessorial) and vaginal sections is recognized, although between the opening of the common oviduct and the openings of the bursa copulatrix and accessory glands is found the vaginal apodeme.

ACCESSORY GLANDS

A pair of glands (parovaria, colleterial glands, caeca) opens from a common stalk close to the opening of the bursa copulatrix, in all of the tipulines studied, except in *Dolichopeza*, as reported by Byers (1961), where they open onto the basal portion of the bursa copulatrix. These glands assume various shapes (Figs. 75-81) in the different species studied, and their opening, which is usually a common stalk and which would be equivalent to the caecal atrium (Abul-Nasr, 1950), may be well removed from the opening of the bursa copulatrix as in *Tipula* (*Lunatipula*) *unicincta* (Fig. 60), a situation comparable to that found in *Panorpa* (Mecoptera). Usually these glands open in the intersegmental membrane between the eighth and ninth sterna; however, this membranous area may become sclerotized as in the aforementioned species (and also in *Panorpa*) and even become specialized in that it becomes swollen ventrally at the openings of the accessory glands and the bursa copulatrix (Figs. 60, 63).

BURSA COPULATRIX, SPERMATHECAL DUCTS AND SPERMATHECAE

Cephalad from the opening of the accessory glands, and occurring also in the intersegmental membrane between the eighth and ninth sterna, is the opening of the bursa copulatrix. In his 1950 paper Abul-Nasr describes what is here termed bursa copulatrix and spermathecal ducts with their terminal spermathecae, but he does not give these parts individual names. I use separate names for the various parts, although they may have a single origin.

The bursa itself is an elongate, cylindrical tube (which is lined by a cuticulum that can withstand the action of potassium hydroxide). At its anterior end it may be curved into a crook as in *Nephrotoma* (Fig. 86), or it may remain straight as in *Tipula* (Fig. 90). In *Dolichopeza* it becomes swollen at its terminus, and for this reason Byers (1961) labelled it the "functional spermatheca," the thought being that perhaps the function of sperm storage is carried out for the most part in this terminal portion.

Somewhat before the terminus of the bursa copulatrix, three slender, elongate and flexible spermathecal ducts arise and lead to balloon-like spermathecae.

OVARIES AND LATERAL OVIDUCTS

A pair of sac-like ovaries is found in the tipulid, and these seem to open directly into a common oviduct. When flies are studied in which the eggs have already been laid, one is tempted to recognize lateral oviducts in a general area where there are what appears to be attenuated ovaries. Whether there are true lateral oviducts present is hard to decide, but gross anatomical observations do not point to this.

A number of incompletely developed eggs may be found in the ovaries of females that have completed oviposition. Bodenheimer (1924) reports that in *Tipula oleracea* from 450-650 ripe eggs are laid and that from 10-30 pink colored eggs which never complete development are frequently found in females after oviposition. Byers (1961) reported that in *Dolichopeza* he could see ovaries with fully-developed eggs in females just emerged from the pupa. In the light of this evidence and the fact that the abdomens of these flies were not swollen it seems highly likely that the females which I studied that appeared to have relatively undeveloped eggs had already oviposited. Some of these females, however, were still teneral and therefore copulation and oviposition must have taken place soon after emergence from the pupa. In addition, the fact

that in crane flies usually all the eggs are deposited at once or in a short period is significant. This condition is suggested by the arrangement of the eggs, which in the tipulines studied almost completely surrounded a common lumen but which in *Dolichopeza* (Byers, 1961) are primarily in a lateral arrangement (Figs. 42, 89).

Each ovary in the specimens of *Tipula* and *Nephrotoma* I have examined ends in a single, long and tapering terminal filament. These filaments seem to extend into the thorax but I could never be sure of their final point of attachment. Bodenheimer (1924) states that they attach to the metanotum. The ovaries when replete with eggs fill the greater part of the abdomen.

COMMON OVIDUCT AND ITS LATERAL ACCESSORY GLANDS

Each ovary joins the common oviduct in the eighth abdominal segment; the common oviduct opens into the genital chamber, the gonopore being located in the membrane between the eighth sternum and the vaginal apodeme.

The common oviduct in its basal half (nearest to the gonopore) is ensheathed by a strong coat of circular muscles. In *Dolichopeza* (Byers, 1961) this ring of muscles is not strongly developed. At the base of the common oviduct there appears a pair of lateral outpocketings. To my knowledge these have not been reported in crane flies, although Potter (1938) reported similar outpocketings in Mecoptera. She called these lateral accessory glands. I could not find these outpocketings in *Dolichopeza*, but they were seen in all the other tipulines examined. Whether they are in actuality glandular is not clear. One must carefully dissect away the greater part of the muscle coat in order to see these structures. The common oviduct (Fig. 59) opens into the genital chamber at the gonopore, which is situated below the openings of the bursa copulatrix and the accessory glands.

Immediately in front of the gonopore and surrounding it on three sides is a rim-like outpocketing of the membranous portion of the eighth sternum. In addition, immediately posterior to the gonopore is a single cushionlike outpocketing of this same membrane. This cushion fits into the open side of the first outpocketing and is thus capable of closing the gonopore (Fig. 62).

It is interesting to note the similarities which exist in features of the internal anatomy of the female reproductive system of the crane fly and that of the bittacid (Mecoptera). The reproductive system in the bittacid has a pair of ovaries similar to those of *Dolichopeza*

(as figured by Byers, 1961), a set of accessory glands opening on a common stalk and separate from the opening of the bursa copulatrix as in *Tipula*, and a pair of lateral accessory glands at the base of the common oviduct; the only striking difference is the presence of but one spermatheca. The male's internal anatomy bears a striking resemblance to that of the crane fly *Dicranomyia chorea*, although the bittacid has the testes divided into four spindle-shaped sperm tubes.

NOTES ON THE HISTOLOGY OF THE FEMALE REPRODUCTIVE SYSTEM

Bauer (1933) has made a detailed study of the structure and development of the ovary of *Tipula paludosa* Meig. The important facts gleaned from this paper are here presented. The germinative cells of the larval ovary of *Tipula paludosa* are surrounded by a peritoneal sheath, a tunica propria, and the ovarian epithelium. Continuous with the ovarian epithelium are the terminal filament and the oviduct. The terminal filament is strongly developed within the body of the ovary and is derived from epithelial cells. This terminal filament is, however, not formed by the union of ovariole filaments as in the case of the grasshopper. Within the body of the ovary are found groups of oögonial cells separated from each other by small cells. Each oögonial cell divides by mitosis into sixteen cells forming groups (Eianlagen); this development goes to completion in the larval stages. Further proliferation of these cells does not take place. In the pupa an egg calyx is formed. Subsequently, the Eianlagen, which are surrounded by a follicular epithelium, become attached to this egg calyx by means of cells which form small stalks. During development, the numerous Eianlagen make random movements within the ovary and become attached to each other by small cell stalks similar to those which attach the Eianlagen to the egg calyx. For this reason one cannot say that true ovarioles are formed but rather egg chains or pseudovarioles. It can be seen from this that the eggs of any one chain do not originate from any one group of germinal cells confined within a germarium. Growth of the egg cells is accompanied by an enlargement of the nuclei. The nutritive cells do not show any increase in size. A secondary muscular sheath which envelops the ovary is derived from cells which are loosely connected, and tracheae lie appressed to the ovary and penetrate it as well. The dioecious ovaries of *Aphidius* and of the Coccidae have nothing in common with those of the crane flies.

The following notes concerning the histology of the female re-

productive organs of *Tipula oleracea* were obtained from Bodenheimer (1924). The "Leitungsapparat" is composed of an "Eiergang" (common oviduct) and a "Vagina" (genital chamber). In the first portion of the common oviduct one finds a thin cubical epithelium surrounded by a coat of longitudinal muscle fibers, which is further surrounded by a very weak sheath of circular muscle. In the second half of the common oviduct the innermost epithelial layer becomes developed into what is described by Bodenheimer as "Zotten," or villous epithelium. This part of the common oviduct is covered by a very strong coat of circular, striated muscles. It is at this point that I have observed the lateral accessory glands, but Bodenheimer apparently did not recognize them in *Tipula oleracea*. Bodenheimer states that at the point where the common oviduct gives way to what is in this paper recognized as the genital chamber the epithelium again becomes more or less cubical and develops a chitinous intima clothed with small, thin hairs.

The ducts of the three spermathecae (receptacula seminis) join to form a common conduit the bursa copulatrix (ductus spermaticus). Each spermatheca is covered by a glandular epithelium and lined with a chitinous intima. Dufour (1851) interpreted the spermathecae as sebaceous glands (glandes sebifiques). Since these organs have been observed to become filled with sperm cells they are more properly considered receptacula. The epithelial tissue covering them is unevenly developed and is composed of columnar cells which contain large nuclei, are rich in vacuoles and are deficient in plasma. This glandular epithelium continues as a covering over the spermathecal ducts. The spermathecae are irregular in shape in *Tipula oleracea*, according to Bodenheimer; I find that they may be uniformly spherical in some other flies.

Leydig (1883), studying *Calliphora erythrocephala* (Diptera: Calliphoridae), wondered why a glandular material should be formed over a chitinized intima. He assumed, as one would have to, that there must be many pores in this intima if the glands were to serve a secretory purpose. Bodenheimer (1924) states that he could find, in the spermathecal intima, many such pores which had diameters ranging from 1-2 microns. Where the epithelium was thickest he observed the greatest number of pores, as might be expected.

The lumen of the bursa copulatrix is larger than that of the spermathecal ducts, and the chitinous intima is thicker. He states that the epithelium is thin but is raised in a ring-like band by virtue

of its nuclei which are intensively colored. It is covered by smooth circular muscle.

The accessory glands (Ectadenien, Kittdrüsen, parovaria, colleterial glands), were misinterpreted as seminal reservoirs (reservoirs seminaux) by Dufour (1851). Bodenheimer states that the epithelium of these glands is composed of a flat, thin, tissue, rich in vacuoles and lacking any chitinous intima. Within may be found a slimy substance (schleimiges Gerinnsel) but never a trace of an admixture of sperm. I have no information concerning the exact function of these glands, so to call them glands is perhaps, at this point, not strictly justifiable. That they are well-developed in females of species that lay their eggs by digging into the soil with their ovipositors as well as in non-digging forms, such as *Tipula bicornis*, would suggest that they have nothing to do with lubricating the ovipositor.

My gross anatomical observations of the ovaries of species in the genera *Tipula* and *Nephrotoma* are in agreement with those of Bauer (1933). Similar observations made by Byers (1961) for *Dolichopeza* suggest the development of ovarioles in a lateral arrangement. Whether these ovarioles are developed in the same manner as those of *Tipula paludosa* cannot be stated at this point.

DISCUSSION

During this study seventy-nine species of Tipulinae were examined. Representatives of the two remaining subfamilies of Tipulidae (Limoniinae and Cylindrotominae) were examined for purposes of comparison. Conclusions drawn from this study are based almost exclusively on characteristics of the genitalia, wing venation being relied upon to some extent to provide additional supporting evidence. While the genitalia provide many good characters upon which to base a classification, sole reliance on such a complex is unwise. The correlation of additional morphological information in the adults coupled with similar data for the larvae and pupae, as well as biological studies, can lead to the best possible taxonomic treatment of any group. Despite these considerations, similarities in structure in and between various subgroupings of this subfamily can be pointed out. Table 6 indicates relationship as suggested by resemblance but should not be regarded as a phylogenetic tree. The scheme attempts to associate forms which show morphological similarities. I believe that there can be observed a gradual and general increase in complexity in the genitalia as one progresses from top to bottom of the tabulation.

TABLE 6.—Scheme of Relationships Based on Genital Characters.

Longurio; *Megistocera*; *Brachypremna*

Nephrotoma; *Dolichopeza*

Tipula (*Trichotipula*)

Tipula (*Nobilotipula*); *Tipula* (*Schummelia*)

Tipula (*Nippotipula*)

Ctenophora; *Tanyptera*; *Holorusia*; *Prionocera*; *Tipula*
(*Arctotipula*)

Tipula (*Yamatotipula*); *Tipula* (*Vestiplex*)

Tipula (*Tipula*)

Tipula (*Oreomyza*) *trivittata* group; *Tipula* (*Oreomyza*) *borealis* group

Tipula (*Lunatipula*); *Tipula* (*Hesperotipula*)

Tipula (*Eumicrotipula*)

By complexity is meant deviation from a simple form (the simple form occurring more often than the complex in the flies I have studied) or one that occurs widely in the group. A few examples illustrate the presence of simple and complicated structures in the same group. In the male *Longurio* we find the basimere free from the ninth sternum, a condition that is widespread in the Limoniinae as well. On the other hand the basimere may become enveloped by the ninth sternum, as in the subgenus *Yamatotipula*, so that the point of union of these two parts cannot be observed externally. The latter form seems more specialized. The adminiculum may be an unmodified, sclerotized projection of the ninth sternum in *Yamatotipula*, whereas it becomes greatly modified in *Lunatipula*, as may be seen by comparison of *Tipula* (*Yamatotipula*) *albocaudata* with *Tipula* (*Lunatipula*) *australis*. The latter form shows in this structure "specialization," which I wish to stress is not intended to indicate a more recently evolved phenomenon, although this may in fact be the case.

Earlier in this paper discussion of the eighth sternum and ninth tergum and sternum of the male was deferred. A few words may now be said concerning these parts. Figures 25, 104 and 105 show variations in the eighth sternum. Between sterna eight and nine of males one frequently observes "lobes," which may be strongly developed (possibly functioning in copulation) and equipped with a musculature or moving by virtue of their close proximity to sclerotized plates which may also serve for the attachment of muscles. Lobes of this sort are commonly found in the subgenus *Lunatipula*. In this same subgenus one may observe other lobe-like processes,

varying in their shape and size and arising from the region of the ninth sternum. These I have called fragmenta of the ninth sternum (following Rees and Ferris, 1939). Comparison of the subgenera *Oreomyza* and *Lunatipula* suggests that such fragmenta may explain the origin of the so-called lateral appendages of the dististyle (used by taxonomists) in the *borealis* group of *Oreomyza*. Species of the *trivittata* group of *Oreomyza* lack the lateral appendages found in those of the *borealis* group and in addition show a tendency toward reduction of the basimere. In the *borealis* group the development of these appendages seems to be correlated with complete reduction of the sclerotized body of the basimere, this area being wholly membranous except for the basal rim, to which muscles are attached. Such a reduction would seem to allow freer movement of the appendage. Furthermore, this suggests that the *borealis* group is derived from the *trivittata* group. Strong development of the fragmenta into pendant lobes is present also in the subgenus *Tipula* and can be seen in *Tipula* (*Tipula*) *pendulifera*. In this group the ninth tergum and sternum are united, suggesting a relationship to *Yamatotipula* and *Vestiplex*. The presence of fragmental lobes may represent a parallelism with the *borealis* group of *Oreomyza*.

The sternal region of the subgenera *Tipula* (*Yamatotipula*) and *Tipula* (*Oreomyza*) has a strong tendency toward development of a median membranous area. In the species of *Tipula* (*Tipula*) I have not found this condition so far advanced.

The ninth tergum is variously modified throughout the Tipulinae; I have figured only a few variations (Figs. 123-127) in the subgenus *Yamatotipula*. Reference can be made to taxonomic works, such as those of Alexander, where the shape of the ninth tergum enables the taxonomist to identify readily many species. There is a median forked projection on the undersurface (morphologically caudal) of the ninth tergum in all three forms of *Tipula* (*Tipula*) examined. See Figure 18 of *Tipula* *spenceriana*. Presence of a tergal "saucer" at the tip of the ninth tergum is quite characteristic of the subgenus *Vestiplex* of *Tipula*. A modification of a comparable area occurs as well in species of the *borealis* group in *Tipula* (*Oreomyza*), though in the latter the tip, while heavily sclerotized, is turned down, not up as in *Tipula* (*Vestiplex*). In *Tipula* (*Vestiplex*) the basimeres are quite distinct, the median line of the ninth sternum is membranous, and the adminiculum is well-developed though simple. In the single species I examined, *fultonensis*, one may observe that the adminiculum is apparently divided medially by membrane.

Such a division has in the past led some morphologists to conclude that it represented two gonapophyses closely appressed, but such a conclusion seems unnecessary in view of the fact that the median line of the ninth sternum in so many forms has become membranous.

In the few species of limoniines examined (*Erioptera*, *Epi-phragma*, *Limonia*, *Pedicia*) the intromittent organ is a straight, tube-like process. A similar condition exists in *Brachypremna*, *Megistocera* and probably also in *Longurio*, which is in other characteristics similar to *Brachypremna* and *Megistocera*. It seems highly probable that this form of intromittent organ represents the basic type in crane flies and that all other types have evolved from it. The intromittent organ of *Tipula* (*Nippotipula*) *abdominalis* is superficially similar to the one already mentioned but differs markedly in features of the aedeagus (Figure 7). I have examined only one cylindrotomine, *Phalacrocera tipulina*, as well as figures of the genitalia given by Peus (1952). In this species further modifications have taken place, such as the development of a tripartite aedeagus, but in other general aspects the intromittent organ as well as the semen pump resemble those of all the tipulines studied, with the exception of those already mentioned. In *Phalacrocera* the semen pump is not rotated dorso-caudally and therefore does not cause the arc characteristic of the aedeagus in *Tipula*, *Nephrotoma*, *Holorusia*, etc.; however, the semen pump does agree well in other aspects with these genera.

With but slight modifications of the wings in the genus *Nephrotoma* (reduction of Sc 1 and loss of R1 + 2), we can derive the wing of *Dolichopeza*. Features of the internal anatomy of the reproductive system show other similarities, including reduction in the size of the semen pump in *Nephrotoma*, with relative increase in the size of the immovable apodemes and compressor apodeme. When the semen pump is reduced in size the compressor apodeme is partially forced out and appears to lie on top of the body of the pump. This feature is common in the genus *Nephrotoma*. The compressor apodeme is cleft in the bulk of tipulines; however, it may lack a pronounced cleft in *Nephrotoma* and *Holorusia* and may show no cleft in *Dolichopeza*. Intermediate forms occur in *Dolichopeza* and *Nephrotoma*.

Running cephalad from the adminiculum of *Dolichopeza* there are two well-developed sclerotizations in the genital sac (adminicular rods, Byers, 1961) which extend to the semen pump and which act as a fulcrum for its rotational movement. In this genus the

sclerotizations are quite pronounced. I have found similar sclerotizations in *Nephrotoma* (*ferruginea*, *euceroidea*), but they are by no means as well developed and are visible only as faint longitudinal lines, quite easily overlooked.

Characteristic of *Dolichopeza carolus*, *venosa*, and *subvenosa* is the development of an intromittent organ of large bore. In *Nephrotoma* the exact opposite has occurred, this organ frequently appearing attenuated and much lengthened. It may extend far into the abdominal cavity causing the genital sac to become correspondingly lengthened. In *Nephrotoma ferruginea* it extends to the anterior margin of the fifth abdominal segment where it then bends caudally in a small arc and runs caudally to its point of emergence. This elongation of the intromittent organ seems characteristic of the genus as a whole; however, it occurs also in other species (*Tipula bicornis*, *Tipula macrophallus*).

In this connection there is an interesting similarity between *Tipula* (*Trichotipula*) *macrophallus* and the genus *Nephrotoma*. The species was described by Dietz, who placed it in *Pachyrrhina* (now *Nephrotoma*). Although it can now be shown to fall within the genus *Tipula*, subgenus *Trichotipula*, its internal anatomy suggests a close relationship to *Nephrotoma*. Other workers have in the past considered *Trichotipula* to be very closely related to *Nephrotoma*. The intromittent organ is developed in a way identical to that of *Nephrotoma* and its length exceeds that of this part in any species of *Nephrotoma* I have examined, extending well into the thorax before turning caudad. The bursa copulatrix in the female of this species is proportionately long.

Tipula (*Nobilotipula*) *nobilis* possesses a robust intromittent organ similar to that found in *Dolichopeza carolus*, *venosa*, and *subvenosa* and in addition has sclerotizations in the genital sac which run cephalad from the adminiculum to the semen pump. The telomeres of *nobilis* are like those of *Dolichopeza*.

Among the species studied in the genus *Nephrotoma* were seen two distinct lines of modification of sternal and basimeral areas. In *Nephrotoma ferruginea* the basimere is not reduced in size, in comparison with other *Nephrotomas*, and the tergum and sternum extend approximately the same distance from their respective antecostae. Lines possibly radiating from this stem are as follows: 1) the sternum is extended caudally while the basimere is reduced in size, as in *Nephrotoma euceroidea* and *polymera*; 2) the sternal region becomes uptilted while the basimere is reduced in size, as

in *Nephrotoma lugens* and *erythrophrys*. The adminicula in *Nephrotoma euceroidea* and *polymera* bear a great resemblance to each other, and this too may indicate a group characteristic.

A form resembling the supposed prototype occurs in *Nephrotoma macrocera*, *virescens*, *punctum*, *xanthostigma*, and *breviorcornis*. Even in these species one can detect the beginnings of sternal enlargement, but these species do not fit in either of the two supposed derived groups on the basis of this feature.

Tipula (Trichotipula) oropezoides, as the name implies, resembles the subgenus *Oropeza* of the genus *Dolichopeza*. In addition to their over-all similarity there is a resemblance in the possession of lobelike appendages at the level of the adminiculum. There is a strong resemblance in the adminicula of *Tipula oropezoides* and *Nephrotoma xanthostigma*.

In the subgenus *Schummelia* I have been able to examine *T. hermannia*. This species resembles *Dolichopeza* in the development of short lobe-like evaginations of the ninth sternum (gonapophyses, Byers, 1961) on either side of the adminiculum. The genital sac possesses the longitudinal sclerotizations as are found in *Dolichopeza*. The supportive sclerite of the semen pump arising from the posterior immovable apodemes is well developed, a condition seen in *Nephrotoma* as well. In *Tipula hermannia* the semen pump and associated apodemes are quite distinct, and there is a median cephalic inflection and fusion of the posterior immovable apodemes in a fashion not observed in any other tipuline.

The reproductive structures in the genera *Holorusia*, *Ctenophora*, *Tanyptera*, *Prionocera*, and the subgenus *Arctotipula* of *Tipula* appear quite similar, as shown by the telomeres, the simplicity of the adminiculum, the absence of fragmenta, and the lack of median weakness in the ninth sternum such as is found in *Tipula (Yamatotipula)*. In the species examined in these groups there is partial fusion of basimere and sternum. *Tanyptera topazina* has the ninth sternum inflected in the midline causing the otherwise unmodified adminiculum to be pushed cephalad. In *Ctenophora apicata* a portion of the ninth sternum is produced caudad without causing any resulting displacement of the adminiculum.

It is difficult to place *Nippotipula* in the scheme. *Tipula (Nippotipula) abdominalis* is a most uncomplicated form as regards its external morphology. It lacks specialization of the sternum and possesses unmodified telomeres; in fact the telomeres are perhaps the least modified of all species examined. It seems to be compara-

ble to forms such as *Ctenophora*, but any further comments would be highly speculative. Most outstanding are its distinctive semen pump and intromittent organ (Fig. 7).

Yamatotipula and *Vestiplex* are placed near each other primarily because they lack a separation between the ninth tergum and sternum. Both groups show membranization in the midline of the ninth sternum but this is more pronounced in *Yamatotipula*. Loss of median sclerotization of the ninth sternum is observed also in *Tipula* (*Oreomyza*), and in addition an uptilting of the ninth segment has occurred. A similar uptilting of the ninth sternum is found in *Yamatotipula*. The development of lateral appendages of the inner telomere, characteristic of the *borealis* group of the subgenus *Oreomyza*, has already been discussed. The ninth tergum and sternum remain divided in *Oreomyza*. Earlier, reasons were given for placing *Tipula* (*Tipula*) close to *Tipula* (*Oreomyza*) on the basis of the development of lateral telomeral appendages. *Tipula* (*Tipula*) is like *Yamatotipula* in having no visible separation of ninth tergum and sternum.

Concerning the last three groups in the scheme the greatest resemblances occur between *Tipula* (*Lunatipula*) and *Tipula* (*Hesperotipula*). Females of the *bicornis* group of *Lunatipula* and those of *Hesperotipula* are remarkably similar, both showing reduction in the ovipositor (cerci and hypovalvae). In addition the males resemble each other in the possession of appendages arising from the intersegmental membrane between the eighth and ninth sterna as well as in fragmental development of the ninth sternum. Males of *Hesperotipula* are further modified in the reduction of the ninth tergum and in the possession of elongate processes arising from the basimere. One can see the beginnings of such basimal development in the *bicornis* group of *Lunatipula* as well. The ninth tergum and sternum are separate in both groups.

The presence of fragmenta in the ninth sternum in the species of *Lunatipula* has enabled me, so far, to recognize all species in this subgenus on sight by this character alone. Diversity in the shape of the adminiculum reaches its extreme in *Lunatipula*, as is readily seen by examining, for example, such species as *Tipula australis*, *mohavensis*, and *bicornis*.

The reasons for placing *Tipula* (*Eumicrotipula*) close to *Tipula* (*Lunatipula*) are the form of the telomeres and the development of the adminiculum. I have been able to examine only a single species of *Eumicrotipula*, *T. chiricahuensis*, and find no other out-

standing resemblances between this species of *Eumicrotipula* and those of *Lunatipula*.

It is hoped that the figures accompanying this text can clarify, to some extent, the information presented. No attempt has been made to illustrate all the species studied, and only partial drawings are given in many cases. The prime purpose of these figures is to enable the reader to locate the characters so that personal observation is facilitated. It is a difficult task to describe characters as diverse in form as are found in the tipulid terminalia, even more difficult to devise groupings on the basis of these characters. I have put down only my impressions. Finally, I wish to say that there is no better way of understanding these features than by personal observation.

SUMMARY

A gross morphological study was made of the reproductive system of 79 North American species of crane flies in the subfamily Tipulinae. Some representatives of the two remaining subfamilies were examined for comparative data. The major results obtained are as follows:

THE MALE REPRODUCTIVE SYSTEM

1. Although the main reproductive organs are on the ninth segment, the eighth is sometimes provided with structures presumably of importance in copulation.

2. The development of the intromittent organ and clasping organs in crane flies seems best explained by the phallic lobe theory, as discussed by Snodgrass (1957). Since gross dissection cannot shed light upon the mode of development of the intromittent organ, two alternative and flexible sets of terminology for the parts of this organ are offered.

3. Evidence of torsion in the terminal abdominal segments of males in the genera *Brachyremna* and *Megistocera* is reported.

4. The semen pumping mechanism is probably derived from proximal elements of the intromittent organ.

5. Two sets of immovable apodemes, which serve as points of attachment for the muscles of a movable apodeme, the compressor apodeme of the semen pump, are derived from the dorsal wall of the genital chamber.

6. The working mechanism of the semen pump and the movement of the intromittent organ are explained by operation of five sets of muscles associated with these parts.

7. The remainder of the male genital tract is composed of a pair of testes, a pair of separate vasa deferentia, a seminal vesicle, a pair of accessory glands originating at the seminal vesicle, a single ejaculatory duct and a large "gland" at the end of the ejaculatory duct where it joins the semen pump.

8. The distribution of muscles to the telomeres does not require an appendicular origin of these structures. While it is impossible by the methods used to decide this point, the author prefers a sternal interpretation of these parts.

9. Three types of relationship between the semen pump and the intromittent organ were observed: a) intromittent organ a straight tube arising directly from the semen pump, b) intromittent organ bowed due to dorsocaudal rotation of the pumping mechanism (semen pump), resulting in the semen pump being dorsal to the intromittent organ, c) intromittent organ essentially straight but with a slight ventral bowing and with a peculiar enlargement of the aedeagus.

THE FEMALE REPRODUCTIVE SYSTEM

1. The segments involved in the female reproductive system are eight through eleven.

2. The functional ovipositor is derived from the cerci and the hypovalvae.

3. The eleventh tergum in female adult Tipulinae is apparently lost; the hypovalvae are thought to be extensions of the eighth sternum.

4. An infra-anal plate may represent the eleventh sternum.

5. A well-developed tenth tergum is present; however, the tenth sternum has apparently been reduced to a membranous area between the ninth sternum and the infra-anal plate.

6. The ninth sternum varies in degree of sclerotization as well as in shape; it is found directly above the eighth sternum and below the level of the infra-anal plate.

7. The vaginal apodeme, a sclerite which is inflected into the body, lies between the eighth and ninth sterna.

8. The remainder of the female genital tract is composed of a pair of ovaries with their terminal filaments, a common oviduct, a pair of lateral "glands" at the distal end of the common oviduct, the bursa copulatrix, opening on the intersegmental membrane between the eighth and ninth sterna, with three spermathecal ducts terminating in bulb-like spermathecae, and a pair of accessory glands usually

opening on a common stalk caudal to the bursa copulatrix, though sometimes directly into the bursa copulatrix. The opening of the accessory glands is located on the intersegmental membrane between the eighth and ninth sterna.

INTRA- AND EXTRALIMITAL RELATIONSHIPS

1. Previously, similarities in the external anatomy of the female reproductive structures of Tipulidae and Mecoptera have been observed (Byers, 1954); the internal organs of these two groups likewise are shown to bear striking resemblances.

2. A grouping of the various genera and subgenera, based on similarities in structure and degree of complexity, of features of the reproductive system and wing venation is given, but no claim is made for the phylogenetic significance of these groups.

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PLATE I

FIG. 1.—Dorsal view of semen pump and associated parts in *Tipula* (*N.*) *abdominalis*, male. Note the enlarged club-shaped specialization of the aedeagus. AIA = anterior immovable apodeme (anteriorly divided); CA = compressor apodeme; SP = semen pump (bulb); ?PIA = though muscles could not be studied due to the fact that only dry museum specimens were available, this part may represent the posterior immovable apodeme; GS = genital sac; Ae = aedeagus.

FIG. 2.—Dorsal view of semen pump and associated parts in *Tipula* (*E.*) *chiricahuensis*, male. scl = sclerotization in dorsal wall of genital sac (epimere, Rees and Ferris, 1939).

FIG. 3.—Lateral view at apex of intromittent organ in *Tipula* (*E.*) *chiricahuensis*, male.

FIG. 4.—Arm of compressor apodeme in *Tipula* (*E.*) *chiricahuensis*, male.

FIG. 5.—Caudal view of semen pump and associated parts in *Holorusia* (*H.*) *grandis*, male. s = small supportive sclerite of the ejaculatory duct.

FIG. 6.—Caudal view of ninth segment, semen pump and associated parts in *Brachypremna dispellens*, male. Note: 1) rotation of segment nine. A = adminiculum; ED = ejaculatory duct; B = basimere; T = telomere.

FIG. 7.—Lateral view of semen pump and associated parts in *Tipula* (*Nipipotipula*) *abdominalis*, male.

FIG. 8.—Caudal view of adminiculum and intromittent organ in *Tipula* (*E.*) *chiricahuensis*, male. Note complexity of adminiculum.

PLATE I

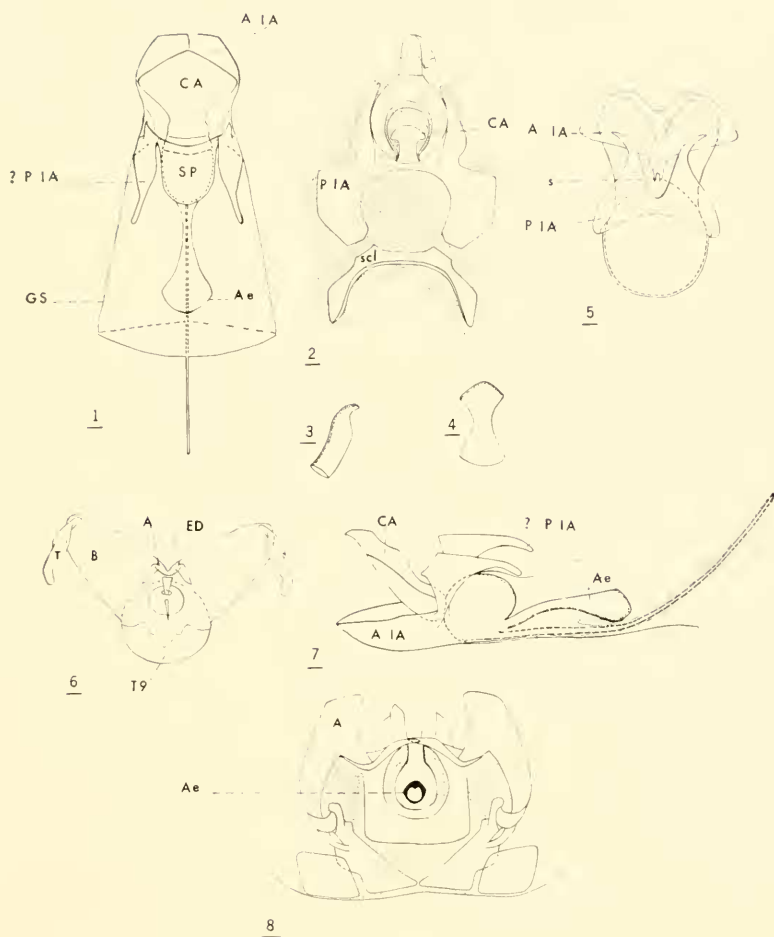


PLATE II

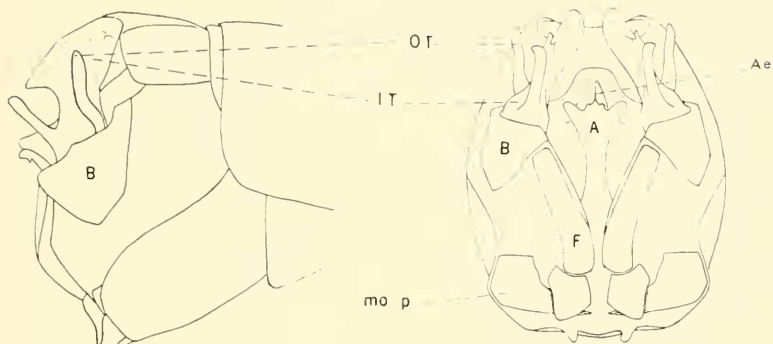
FIG. 9.—Lateral view of terminal abdominal segments in *Tipula* (L.) *triplex*, male. B = basimere; OT = outer telomere; IT = inner telomere.

FIG. 10.—Caudal view of *Tipula* (L.) *triplex*, male. A = adminiculum; Ae = aedeagus; F = fragmentum; mop = movable process of intersegmental membrane between eighth and ninth sterna.

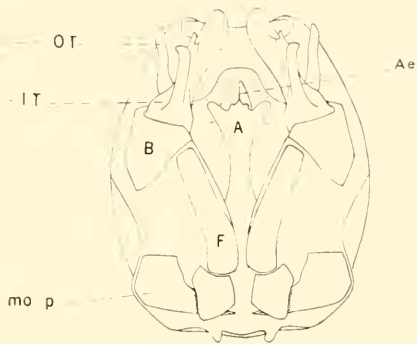
FIG. 11.—Caudal view of ninth abdominal segment in *Ctenophora* (T.) *topazina*, male.

FIG. 12.—Caudal view of terminal abdominal segments in *Tipula* (Nip-) *potipula*) *abdominalis*, male.

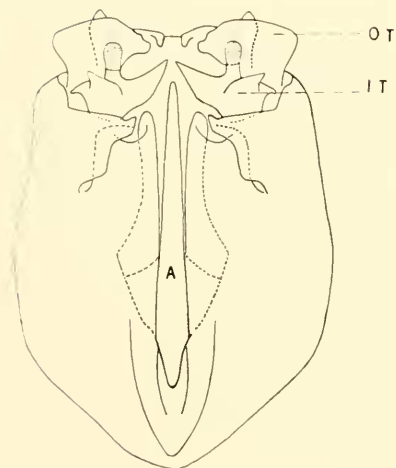
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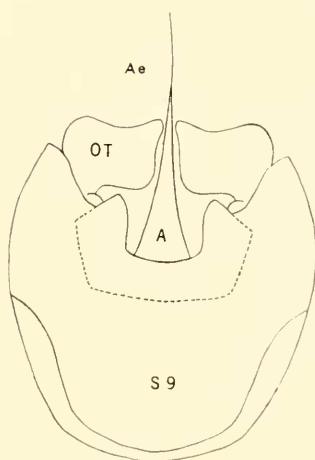
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PLATE III

FIG. 13.—Lateral view of terminal abdominal segments in *Nephrotoma euceroïdes*, male, telomeres removed. Note extension of ninth sternum and development of adminiculum. A = adminiculum; B = basimere; m = an out-pocketing at base of median membranization of ninth sternum.

FIG. 14.—Caudal view of terminal abdominal segments in *Nephrotoma euceroïdes*, male. OT = outer telomere; m = median membranization of ninth sternum.

FIG. 15.—Lateral view of terminal abdominal segments in *Nephrotoma ferruginea*, male. m = base of median membranization of ninth sternum; IT = inner telomere.

FIG. 16.—Caudal view of ninth abdominal segment in *Nephrotoma ferruginea*, male, telomeres removed.

FIG. 17.—Caudal view of ninth abdominal segment in *Nephrotoma lugens*, male, telomeres removed. Note upturning of ninth sternum and fusion of tergal and sternal antecostae (an) into a single process.

FIG. 18.—Caudal view of ninth abdominal segment in *Tipula (T.) spenceriana*, male. Note median, apically divided process (mp) of ninth tergum, general membranization (m), and specialization of ninth sternum: sclerotized processes.

PLATE III

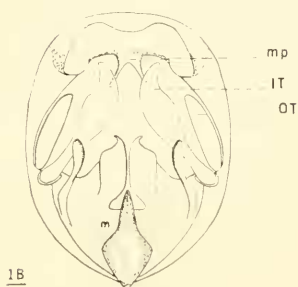
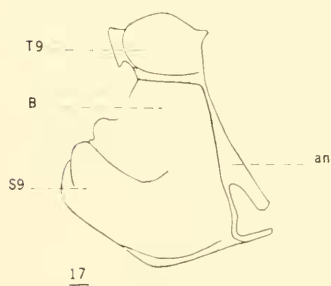
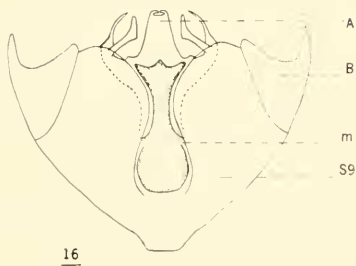
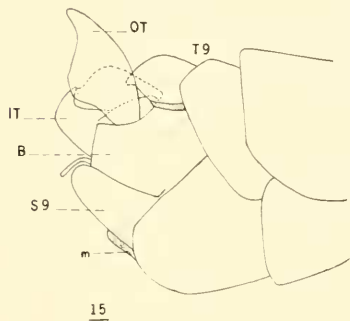
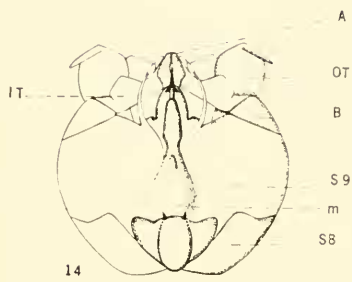
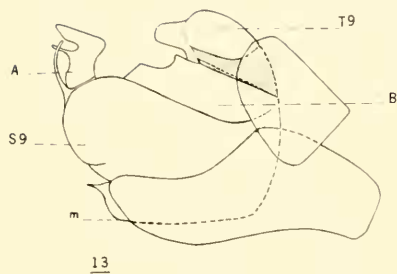


PLATE IV

FIG. 19.—Caudal view of ninth abdominal segment in *Tipula* (Y.) *albo-caudata*, male. m = median membranization of ninth sternum; A = adminiculum; OT = outer telomere; IT = inner telomere.

FIG. 20.—Caudal view of ninth abdominal segment in *Prionocera oregonica*, male.

FIG. 21.—Lateral view of terminal abdominal segments in *Tipula* (Y.) *furca*, male.

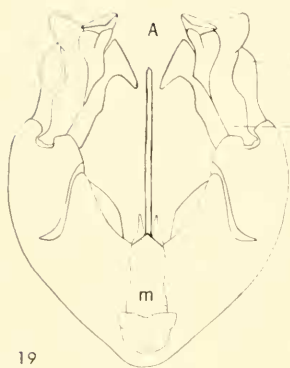
FIG. 22.—Caudal view of ninth abdominal segment in *Tipula* (Y.) *sulphurea*, male, telomeres removed. Note tripartite adminiculum (A) with lateral arms free.

FIG. 23.—Caudal view of ninth segment in *Tipula* (Y.) *furca*, male. Note extent of membranization of ninth sternum (m). Ae = aedeagus; la = lateral arm of adminiculum.

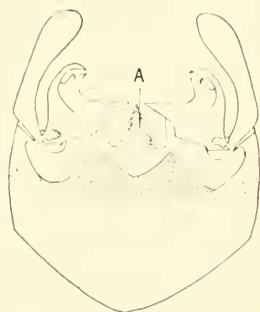
FIG. 24.—Caudal view of intersegmental lobes in membrane between eighth and ninth sterna of *Tipula* (L.) *australis*, male. Note sclerotized plate between these lobes.

FIG. 25.—Caudal view of eighth abdominal sternum in *Tipula* (L.) *australis*, male, showing development of a pair of lobes.

PLATE IV



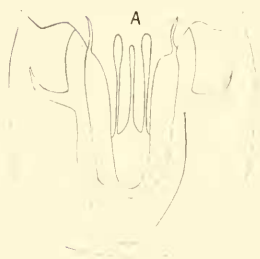
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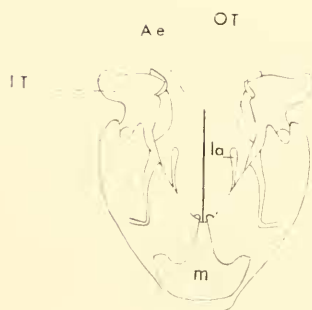
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PLATE V

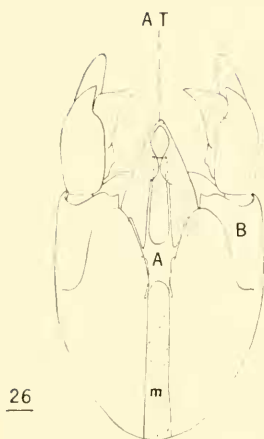
FIG. 26.—Caudal view of ninth abdominal segment in *Tipula* (Y.) *jacobus*, male. AT = membranous anal tubercle (= ?10th and 11th segments); A = adminiculum; m = median membranization of the ninth sternum; B = basimere; OT = outer telomere; IT = inner telomere.

FIG. 27.—Lateral view of terminal abdominal segments in *Tipula* (O.) *trivittata*, male.

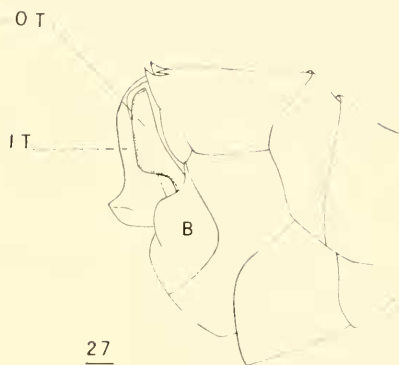
FIG. 28.—Caudal view of ninth abdominal segment in *Tipula* (O.) *borealis*, male. Note development of large appendage (LA) contiguous with inner telomere.

FIG. 29.—Caudal view of ninth abdominal segment in *Tipula* (O.) *borcalis*, male. Note upturning of ninth abdominal segment and reduction of basimere to membrane (B).

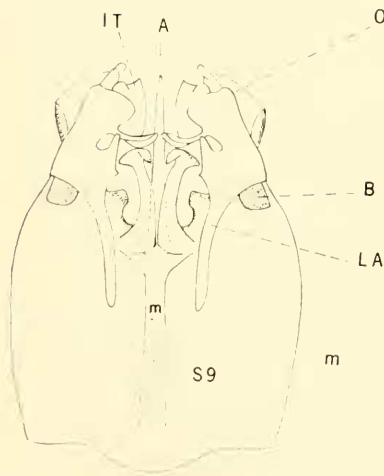
PLATE V



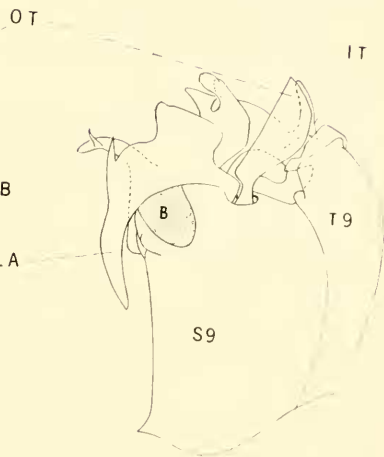
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PLATE VI

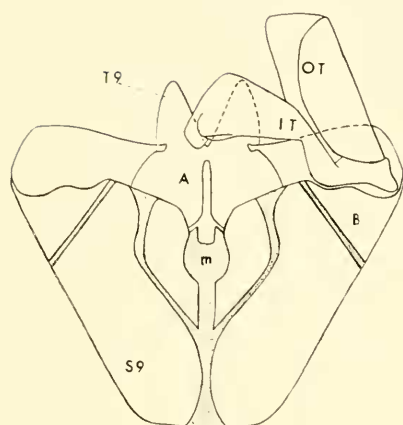
FIG. 30.—Caudal view of ninth abdominal segment of *Holorusia* (*H.*) *grandis*, male left telomeres removed. OT = outer telomere; IT = inner telomere; B = basimere; A = adminiculum; m = median membranization of ninth sternum.

FIG. 31.—Dorsal view (somewhat oblique) of ninth segment in *Tipula* (*H.*) *tryptophora*, male. Note fusion of inner and outer telomeres, reduction in size of ninth tergum, and development of basimere (B) into a long process.

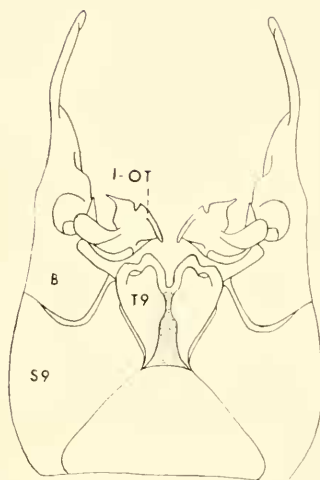
FIG. 32.—Caudal view of terminal segments of *Tipula* (*Nobilotipula*) *nobilis*, female. Note reduction of cerci into small lobes, reduction of sclerotization in ninth segment leaving only two sclerotic bars; openings between "bars" of ninth sternum are of bursa copulatrix and accessory glands; opening to rear of vaginal apodeme (VA) is of gonopore (Go). IP = infra-anal plate; H = hypovalve.

FIG. 33.—Lateral view of *Tipula* (*Nobilotipula*) *nobilis*, female.

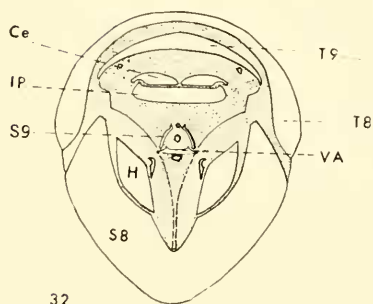
PLATE VI



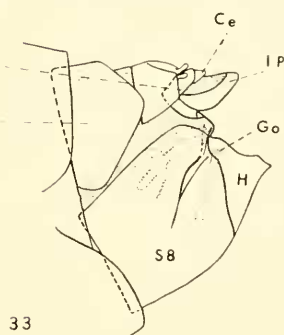
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PLATE VII

FIG. 34.—Lateral view of ninth abdominal segment of *Tipula* (Y.) *spernax*, male. OT = outer telomere; IT = inner telomere.

FIG. 35.—Lateral view of ninth segment of *Tipula* (T.) *pendulifera*, male. Note fusion of ninth tergum and sternum, pendulous lobe or fragmentum (F). B = basimere; T-S9 = fused tergum and sternum of segment nine.

FIG. 36.—Caudal view of ninth segment of *Tipula* (Y.) *spernax*, male.

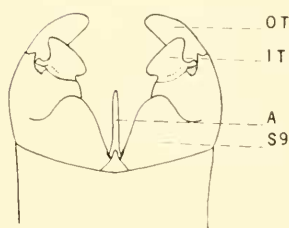
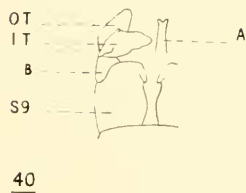
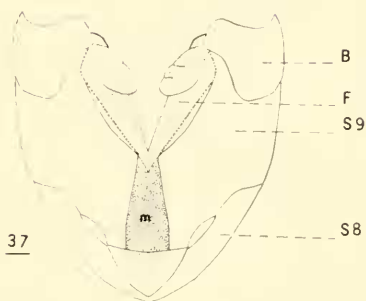
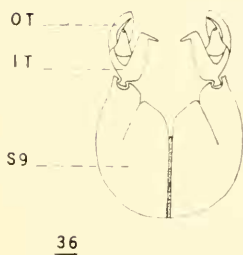
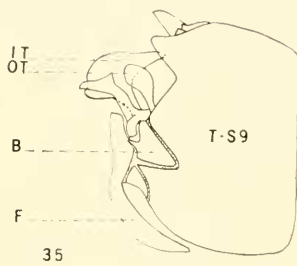
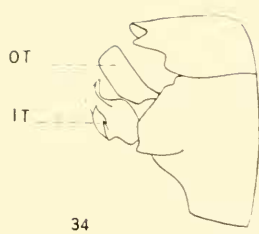
FIG. 37.—Caudal view of terminal abdominal segments of *Tipula* (O.) *pseudotruncorum*, male, telomeres removed. m = median membranization of the ninth sternum.

FIG. 38.—Lateral view of *Tipula* (A.) *semidea*, male. (Redrawn from Alexander, 1954). Note simplicity of telomeres and basimere partially fused with sternum.

FIG. 39.—Oblique ventral view of caudal abdominal segments of *Tipula* (A.) *plutonis absaroka*, male.

FIG. 40.—Ventral view of the ninth abdominal segment of *Tipula* (A.) *semidea*, male. (Redrawn from Alexander, 1954.)

PLATE VII



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PLATE VIII

FIG. 41.—Lateral view of *Dolichopeza (O.) venosa*, male (from Byers, 1961), to show position of semen pump and intromittent organ at rest. sGS = sclerotizations (adminicular rods) of genital sac contiguous with adminiculum (A); p = sternal process (gonapophysis); AIA = anterior immovable apodeme; PIA = posterior immovable apodeme; CA = compressor apodeme; SP = semen pump; Enph = endophallus. Only heavily sclerotized areas are shown in the figure, hence the genital sac is not figured.

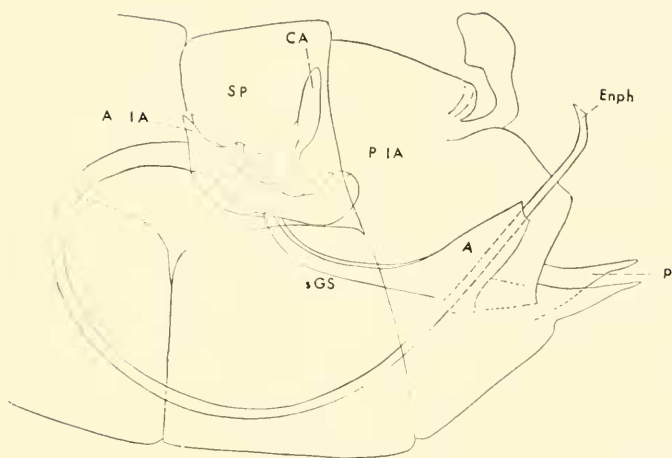
FIG. 42.—Schematic drawing to show internal reproductive features of *Dolichopeza (O.) tridenticulata*, female (from Byers, 1961). spt = spermatheca; dspt = spermathecal duct; fspt = functional spermatheca; bc = bursa copulatrix; abc = aperture of bursa copulatrix; rct = rectum; cr = cercus; acg = accessory glands; gp = gonopore; hv = hypovalve; ovl = ovariole; lov = lateral oviduct; mov = median oviduct.

FIG. 43.—Partial drawings of bursa copulatrix showing connection of accessory glands in *Dolichopeza (O.) carolus*, female. Note: 1) spermathecal ducts cut. (From Byers, 1961.)

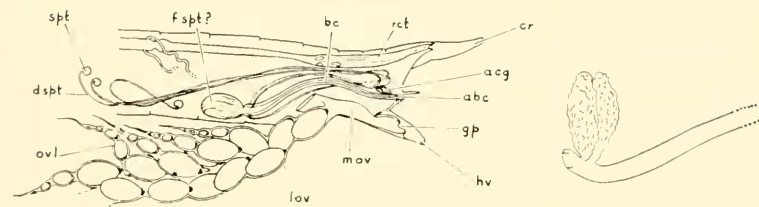
FIG. 44.—Bursa copulatrix, spermathecal ducts, spermathecae and accessory glands in *Dolichopeza (D.) americana*. (From Byers, 1961.)

FIG. 45.—Detail of accessory glands showing their attachment point to bursa copulatrix in *Dolichopeza*.

PLATE VIII



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PLATE IX

FIG. 46.—Cephalic view of semen pump in *Tipula (L.) triplex*, male, showing the relative position of sclerite (scl) ("epimere") in dorsal wall of genital sac. PIA = posterior immovable apodeme; CA = compressor apodeme; b = bulb of the semen pump; AIA = anterior immovable apodeme; Enph = endophallus.

FIG. 47.—Cephalic view of semen pump of *Tipula (L.) triplex*, male showing position of the gland (G) at the base of the ejaculatory duct (ED).

FIG. 48.—Dorsal view of semen pump of *Nephrotoma ferruginea*, male. s = sclerotized brace of the semen pump.

FIG. 49.—Oblique lateral view of terminal abdominal segments of *Tipula (Nippotipula) abdominalis*, male. AT = anal tubercle; sA = sclerites associated with anal tubercle (two dorso-lateral and two latero-ventral sclerites).

FIG. 50.—Detail of gland (G) at the base of the ejaculatory duct (ED). Note sclerotized intima at the base of ejaculatory duct indicated by "ringed" tube.

PLATE IX

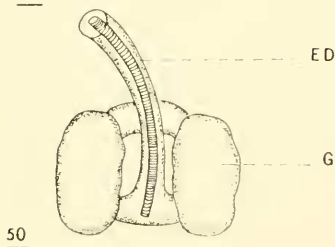
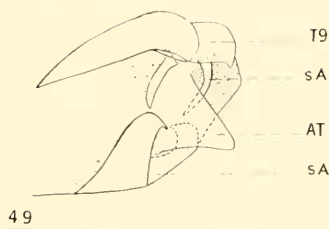
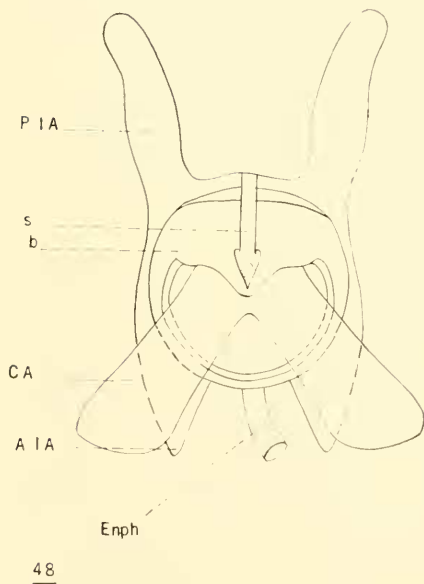
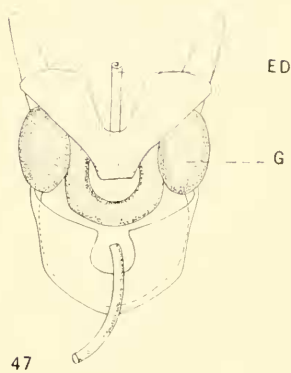
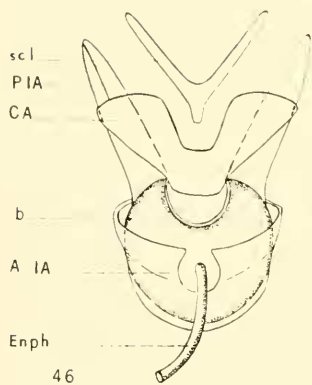


PLATE X

FIG. 51.—Dorsal view of semen pump and intromittent organ of *Brachypremna dispellens*, male. *In situ* these structures are rotated about 180° in longitudinal plane. CA = compressor apodeme; ED = ejaculatory duct; s = supportive sclerite of the ejaculatory duct; GS = genital sac; Ae = aedeagus; Enph = endophallus.

FIG. 52.—Lateral view of semen pump and intromittent organ of *Brachypremna dispellens*, male. AIA = anterior immovable apodeme; ED = ejaculatory duct.

FIG. 53.—Lateral view of semen pump of *Nephrotoma ferruginea*, male. S_1 = semen pump brace; s = supportive sclerite of the ejaculatory duct.

FIG. 54.—Lateral view of the telomeres of *Tipula (O.) latipennis*, male. Note pendulous lateral lobe (LA) of the inner telomere (IT), and membranization of the basimere (B). OT = outer telomere.

PLATE X

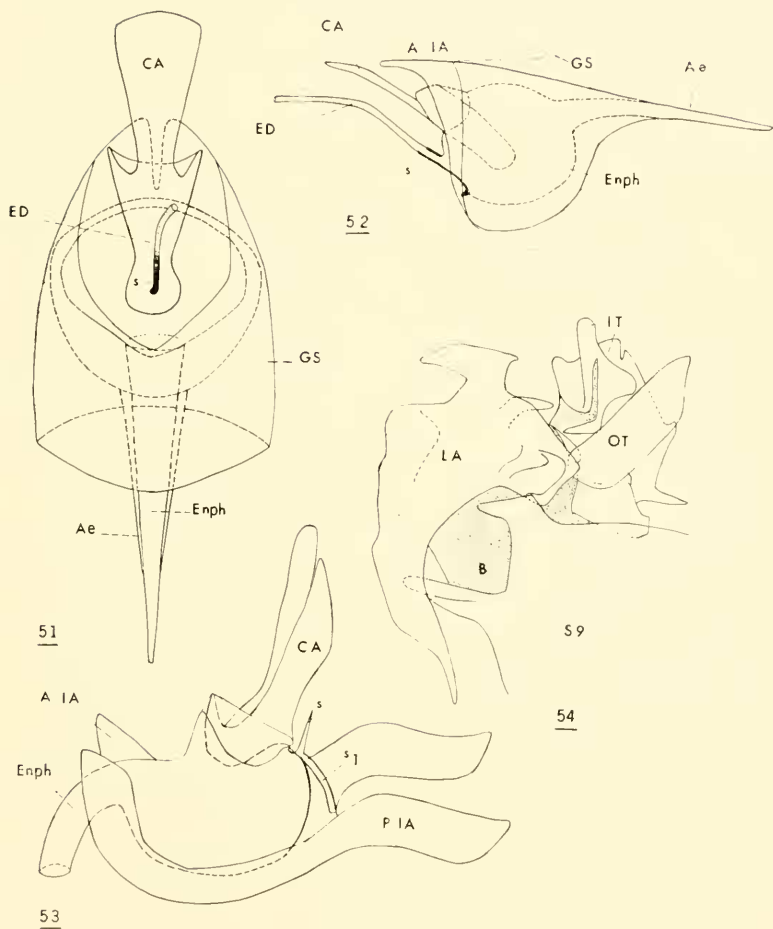


PLATE XI

FIG. 55.—Gross internal features of male reproductive system of *Dolichochepeza*. Total length of accessory glands not figured; dotted line along vasa deferentia indicates unfused but closely appressed tubes; glands at base of ejaculatory duct not figured. TS = testes; VD = vas deferens; AG = accessory glands; SV = seminal vesicle; ED = ejaculatory duct.

FIG. 56.—Gross internal features of male reproductive system. Note slight swelling of vas deferens. Dotted line along vasa deferentia indicates unfused but closely appressed vasa deferentia; glands at base of ejaculatory duct not figured.

FIG. 57.—Schematic drawing of transverse section through seminal vesicle anterior to openings of accessory glands and vasa deferentia. Note close appression of vasa deferentia which are surrounded by a tunic (tunica adipomembranacea, Keuchenius, 1913), not labelled in figure.

FIG. 58.—Semi-diagrammatic lateral view of seminal vesicle showing attachment of accessory glands (AG), vasa deferentia (VD) and ejaculatory duct (ED).

PLATE XI

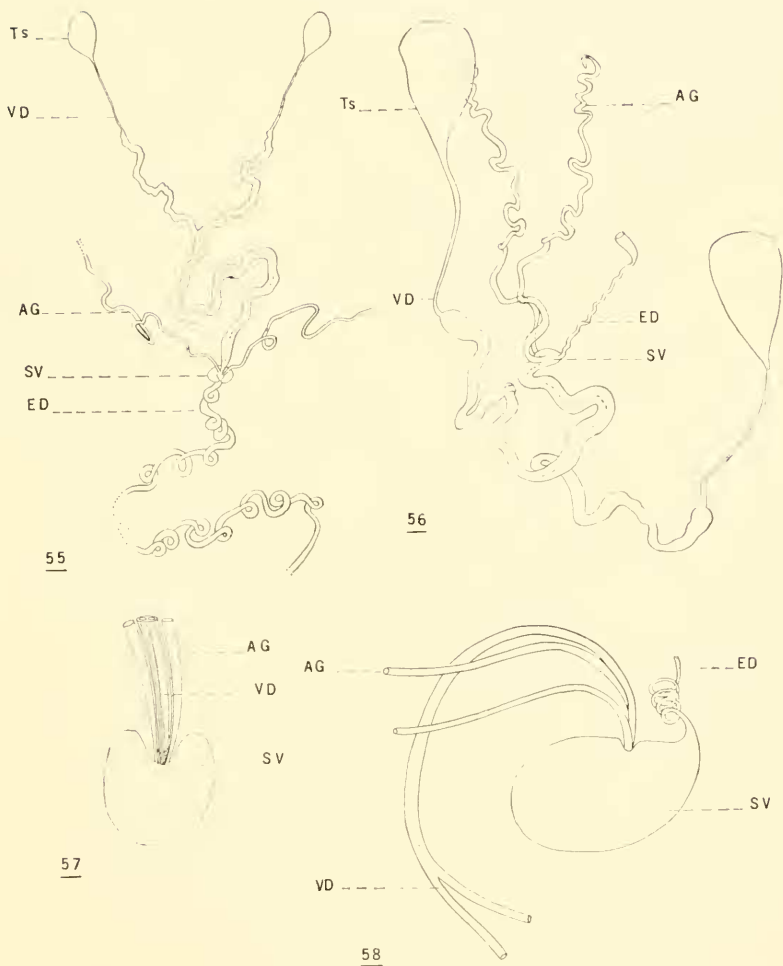


PLATE XII

FIG. 59.—Schematic drawing of terminal abdominal segments of a female tipuline. O = ovary; Sp = spermatheca; T10 = tenth tergum; BC = bursa copulatrix; VA = vaginal apodeme; LAG = lateral accessory glands of common oviduct; CO = common oviduct; Ce = cercus; IP = infra-anal plate; AG = accessory glands; H = hypovalve.

FIG. 60.—Lateral view of ninth sternum and part of eighth at opening of common oviduct in *Tipula (L.) uncinata*, female. Note development of ninth sternum at opening of accessory glands (AG) and at opening of bursa copulatrix (BC).

FIG. 61.—Sclerotization in dorsal wall of genital chamber (epimere) of *Tipula (L.) uncinata*, male.

FIGS. 62 and 63.—Diagrammatic representations of genital chamber and associated parts in *Tipula (L.) uncinata*, female. These two figures are to be used together. In Fig. 62 the openings of the accessory glands, bursa copulatrix and common oviduct are not figured; the openings have been omitted since they are not seen without manipulation of the parts, though the general area is indicated by dotted lines; the accessory glands as well as the bursa copulatrix open on a lobe; the gonopore lies between two padlike evaginations, one fitting into the other and closing the gonopore when this occurs. Go = gonopore.

PLATE XII

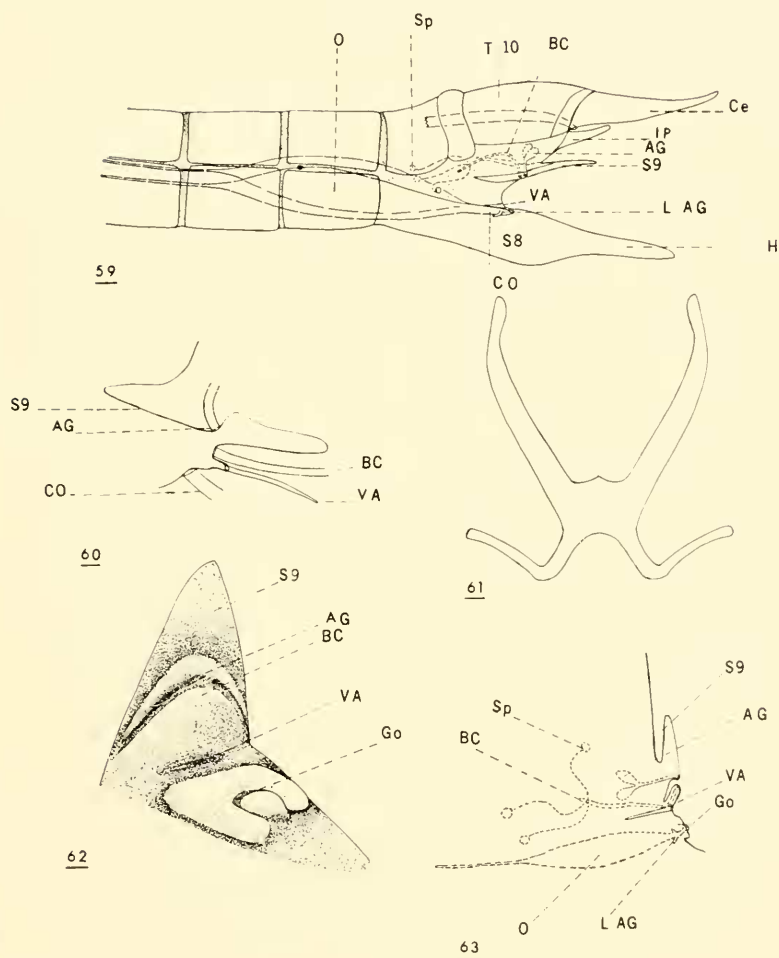


PLATE XIII

FIG. 64.—Ventral view of eighth sternum and hypovalve of *Tipula* (Y.) *sulphurea*, female.

FIG. 65.—Dorsal view of tenth tergum and cerci of *Tipula* (Y.) *sulphurea*, female. Dotted line indicates outline of infra-anal plate.

FIG. 66.—Ventral view of eighth sternum and hypovalvae of *Tipula* (Y.) *spernax*, female.

FIG. 67.—Dorsal view of tenth tergum and cerci of *Tipula* (Y.) *spernax*, female. Dotted line shows outline of infra-anal plate, which is divided.

FIG. 68.—Ventral view of ninth and tenth terga and cerci of *Tipula* (L.) *unicincta*, female, showing musculature. a = muscle from ninth tergal antecosta to antecosta of tergum ten; b = muscle from ninth tergal antecosta to basal rim of cercus; c = muscle from tenth tergal antecosta to basal rim of cercus; Ap = median longitudinal apodemal inflection of tenth tergum. Muscles closely associated with those labelled (c) originate from the median longitudinal apodemal inflection. (See Fig. 69, where they are distinctly separated and labelled d.)

FIG. 69.—Ventral view of ninth and tenth terga and cerci of *Tipula* (L.) *triplex*, female, showing musculature. a = muscle from ninth tergal antecosta to tenth tergal antecosta; b = medially-directed muscle from ninth tergal antecosta to tenth tergal antecosta; c = muscle from tenth tergal antecosta to basal rim of cercus; d = muscle from median longitudinal apodemal inflection of tenth tergum to basal rim of cercus; e = muscle from ninth tergal antecosta to basal rim of cercus; CE = cercus. Whereas in Fig. 68 muscle (c) was singular with two points of origin, *i. e.*, from the tenth tergal antecosta and from the longitudinal median apodemal inflection, in *triplex* this muscle is separated into two muscle groups (c) and (d).

FIG. 70.—Ventral view of ninth and tenth terga, bifid infra-anal plate and cerci of *Tipula* (L.) *triplex*, female.

FIG. 71.—Dorsal view of ninth and tenth terga and cerci of *Tipula* (L.) *triplex*, female.

FIG. 72.—Dorsal view of eighth sternum and hypovalvae of *Tipula* (L.) *triplex*, female.

FIG. 73.—Ventral view of seventh and eighth sterna and hypovalvae of *Tipula* (L.) *triplex*, female.

FIG. 74.—Ventral view of tenth tergum showing divided infra-anal plate (IP) below and caudal cerci of *Tipula* (O.) *latipennis*, female.

PLATE XIII

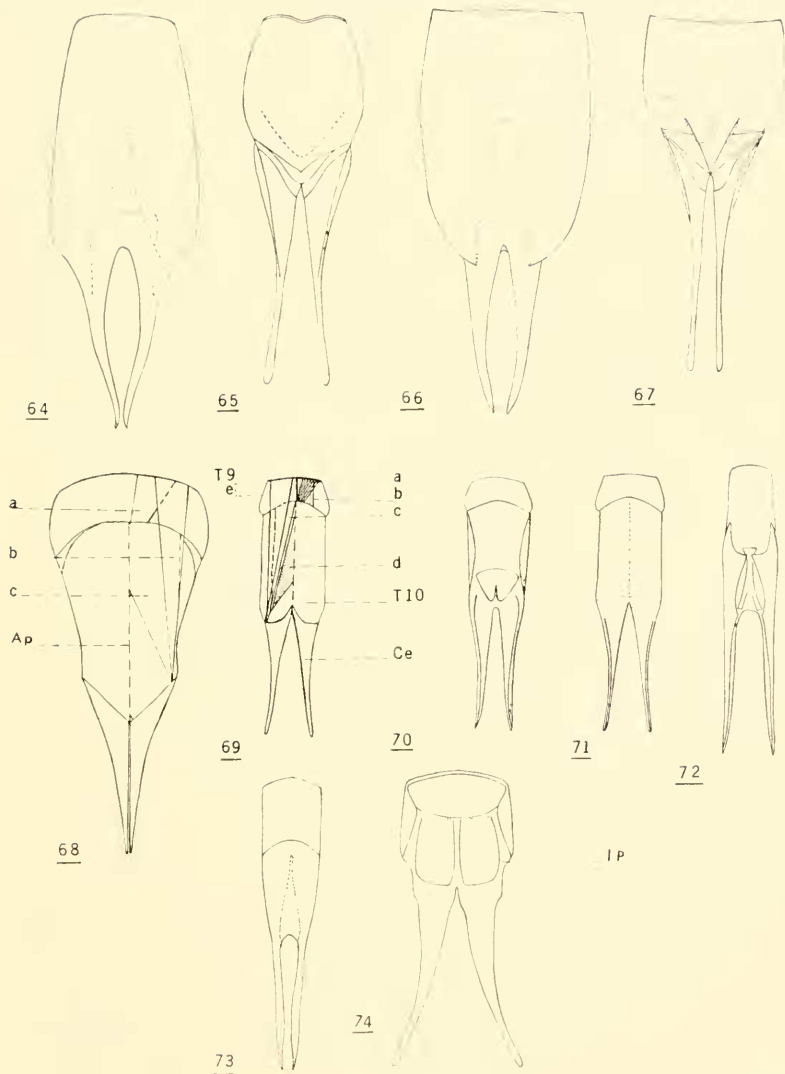


PLATE XIV

FIGS. 75-81.—Accessory glands of females of Tipulinae.

FIG. 75.—*Tipula* (Y.) *triplex*.

FIG. 76.—*Nephrotoma euceroidea*.

FIG. 77.—*Tipula* (L.) *bicornis*.

FIG. 78.—*Tipula* (O.) *latipennis*.

FIG. 79.—*Nephrotoma macrocera*.

FIG. 80.—*Tipula* (L.) *unicincta*.

FIG. 81.—*Tipula* (L.) *furca*.

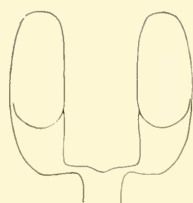
FIG. 82.—Lateral view of terminal abdominal segments of *Tipula* (L.) *bicornis*, female. Note reduction of cerci to lobes and decrease in size of hypovalves. T10 = tenth tergum; Ce = cercus; H = hypovalve.

FIG. 83.—Ventral view of eighth sternum and hypovalve of *Tipula* (L.) *bicornis*, female.

FIG. 84.—Ventral view of ninth and tenth terga showing musculature in *Tipula* (L.) *bicornis*, female. a = muscle from middle of ninth tergum to tenth antecosta; b = muscles from middle of tenth tergum to base of cercus.

FIG. 85.—Dorsal view of terminal abdominal segments of *Tipula* (L.) *bicornis*, female.

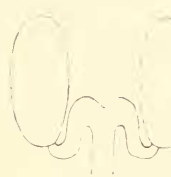
PLATE XIV



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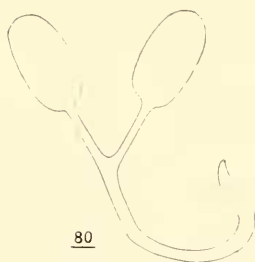
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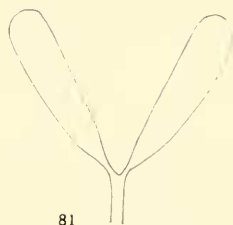
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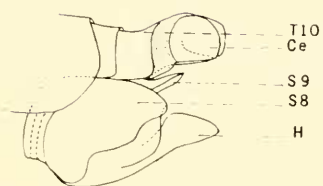
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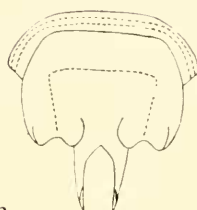
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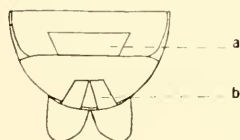
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PLATE XV

FIG. 86.—Internal reproductive system of *Nephrotoma macrocera*, female. SP = spermatheca; SpD = spermathecal duct; BC = bursa copulatrix; AG = accessory glands. Note that bursa copulatrix is curved at its apex.

FIG. 87.—Dorsal view of vaginal apodeme of *Tipula* (Y.) *furca*, female.

FIG. 88.—Apical tip of bursa copulatrix in a *Dolichopeza* female. fSp? = possibly the functional spermatheca, as suggested by Byers (1961).

FIG. 89.—Primary genital tract of a *Tipula* female. TF = terminal filament; O = ovary; CO = common oviduct; LAG = lateral "accessory gland" of common oviduct; GO = level of the gonopore.

PLATE XV

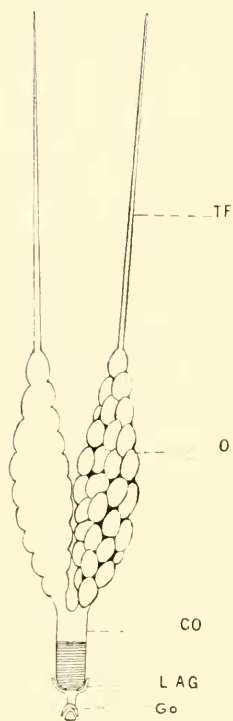
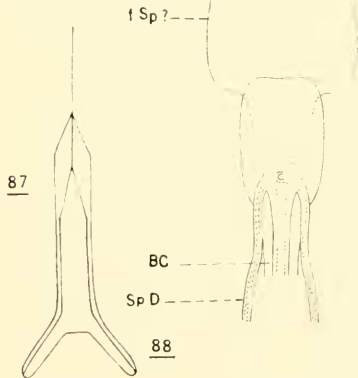
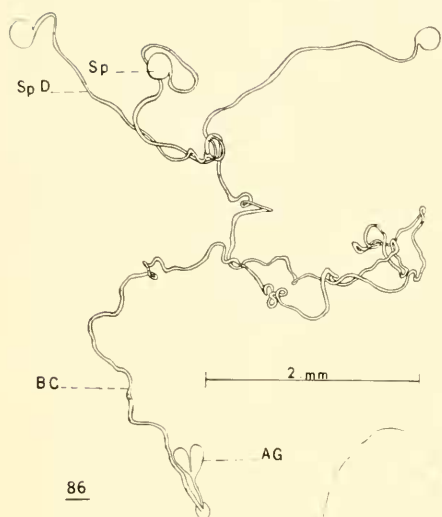


PLATE XVI

FIG. 90.—Ventral view of ninth sternum and associated parts in *Tipula* (L.) *triplex*, female. AG = accessory glands; VA = vaginal apodeme; BC = bursa copulatrix; SPD = spermathecal duct; SP = spermatheca.

FIG. 91.—Internal reproductive system of *Tipula* (Y.) *triplex*, male. Note absence of any swelling in the vas deferens. TS = testes; VD = vas deferens; SV = seminal vesicle; ED = ejaculatory duct; AG = accessory glands.

PLATE XVI

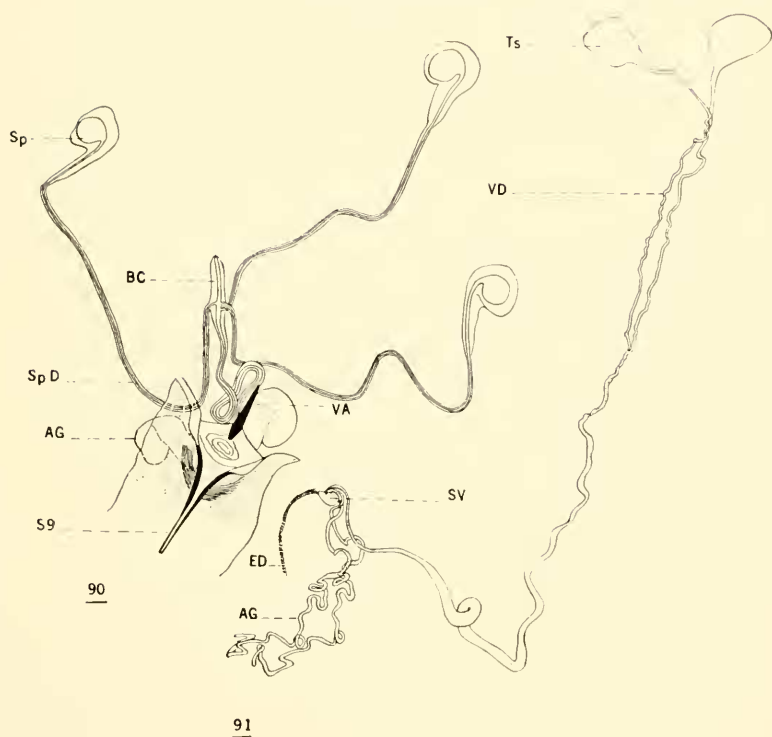


PLATE XVII

FIG. 92.—Caudal view of adminiculum of *Tipula* (L.) *triplex*, male.

FIG. 93.—Caudal view of adminiculum of *Tipula* (Y.) *albocaudata*, male.

FIG. 94.—Caudal view of adminiculum of *Tipula* (Y.) *tricolor*, male.

FIG. 95.—Caudal view of adminiculum of *Tipula* (Y.) *caloptera*, male.

FIG. 96.—Lateral view of a lateral adminicular arm of *Tipula* (Y.) *furca*, male.

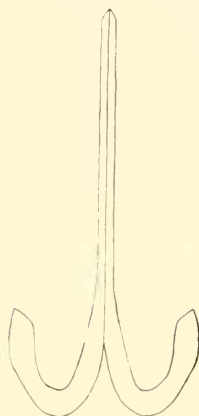
FIG. 97.—Adminiculum of *Tipula* (Y.) *furca*, male.

FIG. 98.—Lateral view of adminiculum of *Tipula* (Y.) *albocaudata*, male.

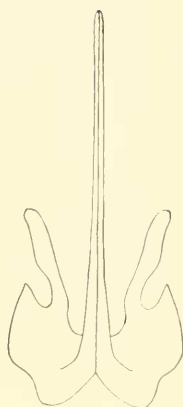
PLATE XVII



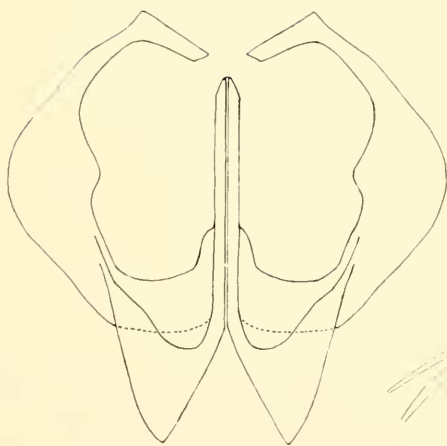
92



93



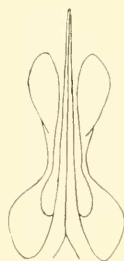
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PLATE XVIII

FIG. 99.—Caudal view of adminiculum of *Tipula* (L.) *bicornis*, male.

FIG. 100.—Vaginal apodeme of *Tipula* (Y.) *tricolor*, female.

FIG. 101.—Vaginal apodeme of *Tipula* (L.) *unicincta*, female.

FIG. 102.—Vaginal apodeme of *Tipula* (Y.) *tephrocephala*, female.

FIG. 103.—Vaginal apodeme of *Tipula* (Y.) *spernax*, female.

FIG. 104.—Ventral view of eighth abdominal sternum of *Tipula* (L.) *triplex*, male. Note two sclerotized processes of the sternum, and movable lobes found in the intersegmental membrane of the eighth and ninth segment.

FIG. 105.—Caudal view of the eight abdominal segment of *Tipula* (H.) *tryptophora*, male.

FIG. 106.—Caudal view of adminiculum (A) and fragmental lobes (F) in *Tipula* (L.) *dietziana*, male.

FIG. 107.—Caudal view of intersegmental membrane between eighth and ninth sterna in *Tipula* (L.) *dietziana*, male. Note median sclerite and lateral lobes.

FIG. 108.—Caudal view of adminiculum in *Tipula* (L.) *australis*, male.

FIG. 109.—Caudal view of adminiculum in *Tipula* (T.) *oropezoides*, male.

FIG. 110.—Caudal view of base of adminiculum in *Tipula* (L.) *mohavensis*, male.

FIG. 111.—Sclerite found in dorsal wall of genital chamber in *Tipula* (L.) *triplex*, male.

FIG. 112.—Shape of sclerotization (only) of anal tubercle in *Tipula* (O.) *latipennis*, male.

FIG. 113.—Dorsal view of the anal tubercle with its sclerotization in *Tipula* (O.) *coloradensis*, male.

FIG. 114.—Ninth sternum of *Tipula* (L.) *triplex*, female.

FIG. 115.—Ninth sternum of *Tipula* (Y.) *jacobus*, female.

FIG. 116.—Lateral view of terminal abdominal segments of *Ctenophora* *topazina*, female. Eighth, ninth, and tenth terga including cerci and infra-anal plate do not show. Note blade-like hypovalve (H). The single, undivided dotted line represents the duct of the bursa copulatrix, while the divided one represents the two accessory glands and their common stalk; the dotted lines below represent the common oviduct.

PLATE XVIII

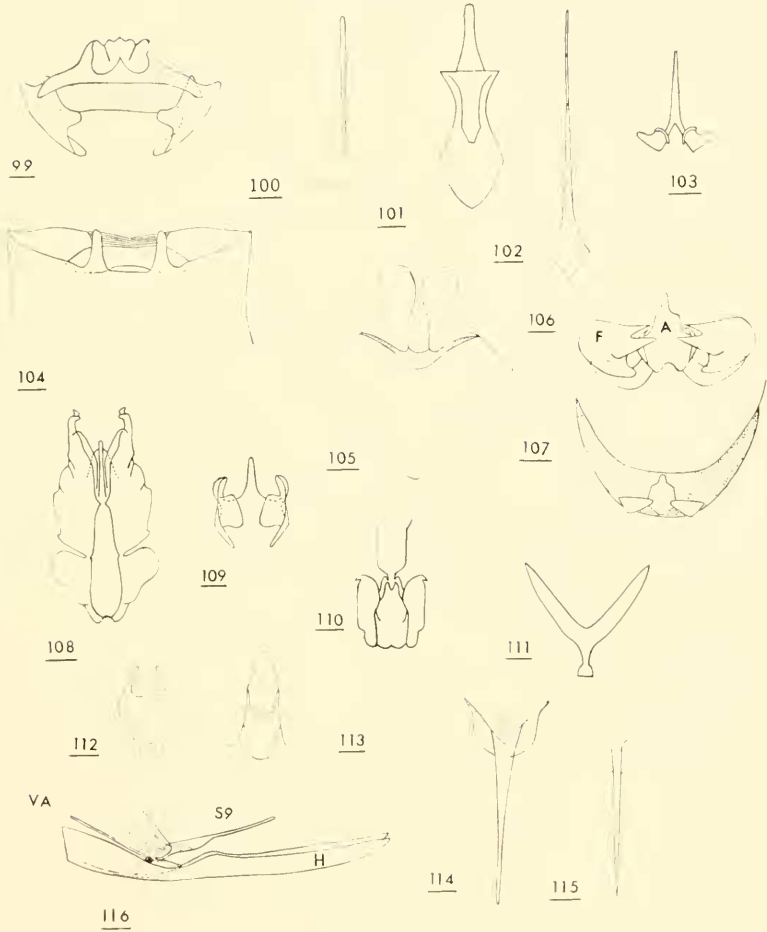


PLATE XIX

FIG. 117.—Dorsal view of ninth sternum of *Tipula* (Y.) *tricolor*, female.

FIG. 118.—Dorsal view of ninth sternum of *Tripula* (Y.) *furca*, female.

FIG. 119.—Dorsal view of vaginal apodeme of *Tipula* (Y.) *caloptera*, female.

FIG. 120.—Dorsal view of ninth sternum of *Tipula* (Y.) *caloptera*, female.

FIG. 121.—Dorsal view of ninth sternum of *Tipula* (Y.) *sulfurea*, female.

FIG. 122.—Lateral view of semen pump and intromittent organ of *Holorusia* (H.) *grandis* male. Note compressor apodeme (CA) between the anterior and posterior immovable apodemes.

PLATE XIX

